THE NITROGEN AND PHOSPHORUS NUTRITION OF *PINUS RADIATA* D. DON

by

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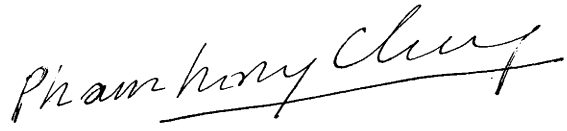
ORIGINALITY OF THESIS

With the exceptions noted in the Acknowledgements, the work described in this thesis is original and was done without collaboration.



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ABSTRACT

The interrelationships of the environment, foliar nutrient levels and growth of Pinus radiata D. Don were examined, particular emphasis being given to nitrogen and phosphorus patterns in the crown.

The horizontal needle age/foliar phosphorus gradient in the crown was characteristic of soil type. A similar but less well defined trend was evident with the nitrogen gradient. Tree vigour did not appear to affect the horizontal gradient or vertical nutrient gradient in current year needles but the evidence suggests that it may affect the extent of seasonal fluctuation in foliar nutrient concentration, especially of phosphorus. Results generally suggest that a healthy vigorous tree on a good site will have moderate horizontal and vertical foliar nutrient gradients and a strong seasonal fluctuation in nutrient levels.

Translocation of phosphorus and nitrogen was more efficient in vigorous than non-vigorous trees and in the latter, phosphorus was the more mobile nutrient. The lower mobility of nitrogen may have implications for dry sites: on these, higher levels of foliar nitrogen (than on moist sites) may be necessary for optimum growth.

Nitrogen uptake is strongly controlled by the availability of phosphorus. If phosphorus is limiting, the foliar nitrogen levels may be high to very high but if non-limiting, the levels will be moderate irrespective of the supply of nitrogen in the soil.

A comparative study of the accumulation and distribution of foliage and branches on low and high quality sites revealed that, on a low quality site at Kowen, A.C.T., the weight of foliage in a P. radiata stand reaches a maximum as early as four to five years of age i.e., well before canopy closure (ca. 12 years), and then declines slowly, at least up to the age of 18 years. Despite this decline in foliage weight, P. radiata crowns are

efficient producers of bole wood on low quality sites, the production per unit of foliage weight being comparable to that on higher quality sites in Australia, at least up to the age of 12 years.

The study also revealed that foliage weight of P. radiata per unit of land area is not independent of stand age, site quality and stand density (as has been found by others e.g., Möller, 1947; Satoo, 1967, for other species), and branch weight after canopy closure tends to increase with increasing site quality, although soil type and possibly climatic conditions may alter the trend.

INTRODUCTION

Australia has a very limited native forest resource, and its wood supply will apparently be increasingly dependent upon plantations of coniferous species. Radiata pine (Pinus radiata D.Don) is the most extensively planted species. The Commonwealth programme is aimed at increasing the plantation estate to 3,000,000 acres by the year 2000. However, there has been a growing concern that productivity of conifer plantations, P. radiata in particular, may not be maintained in the second and later rotations (Keeves, 1966; Bunn, 1967; Lewis, 1967). Hence there has been in recent years a considerable awakening of interest in tree physiology, particularly that of P. radiata (Shepherd, 1965; Wood, 1969). Plantation silviculture and administration in Australia have more often been based on the results of ad hoc trials than a sound knowledge of the species. While in no way decrying the considerable achievements to date, Shepherd (1967) thought that future research will need to be more scientifically based, especially where only marginal increases in productivity can be expected. Florence (1969), for example, in a review of the physical and chemical requirements for growth and yield of forests, suggests that natural selection of individuals particularly adapted to different climatic and edaphic regimes might be one means of improving productivity on marginal sites.

From the point of view of nutrition, there is need for a broad perspective of the role of nutrients in tree development. This broad perspective must include an appreciation of the role of specific nutrients in health and growth of the species, the uptake and redistribution of nutrients within the tree, the efficiency of use of nutrient elements and the way this use is affected by variations in environment, and the influences of nutrients and nutrient balances on growth, not only quantitatively but also qualitatively.

Australian soils available for plantations are frequently deficient in phosphorus. Early work in tree nutrition was

orientated to elucidating this deficiency and establishing guide lines for fertilizer usage (Florence, 1969). Subsequently Richards (1961) for P. taeda, Waring (1962) for P. radiata and others have shown on some sites, additional response to nitrogen may be obtained once the limiting phosphorus deficiency is overcome. Waring (1969) stated: 'Although the present practice, in Australia, of applying phosphorus fertiliser at planting time produces substantial increases in growth and in some cases makes the difference between success and failure of a plantation, the evidence is strong that nitrogen should be added as well. Not only are large production gains possible in the current rotation, but, as the equilibrium point of the soil organic matter is raised, the present trend towards reduction in fertility can be reversed'. However, apart from the widespread response to nitrogen and phosphorus obtained on many soils, deficiencies in a number of other nutrient elements have been recorded but they are generally associated with specific and localized soil conditions, e.g., zinc deficiency on calcareous dune soils (Kessel and Stoate, 1938), potassium deficiency on deep sands or sands over clays derived from parent materials low in K-bearing minerals (Hall and Purnell, 1961), calcium deficiency on one soil derived from a particular sedimentary parent material, within a suite of low phosphorus status solodic type soils (Gentle and Humphreys, 1968), and boron deficiency on granitic and well drained basaltic soils above 2200 ft altitude in Victoria.

Nitrogen and phosphorus therefore are two mineral elements of vital concern in understanding productivity of P. radiata plantations. However, apart from the demonstration of an NxP interaction and the derivation of limiting foliar levels for these nutrients (e.g., Waring, 1962; Raupach, 1967a, b), few studies have been directed to providing the broader perspective of their role in growth and development of P. radiata.

With respect to the role of nutrients in growth and development, the 'philosophy' of Steward (1961) is of interest: 'A true philosophy of plant nutrition emerges not only from an understanding of what each element may uniquely and separately do

but also how they collectively function, not in isolated reaction systems but in the growing cells and meristems of plants. Here interactions between elements are as important as their single effects, as, for example, between K, N and P; Fe and Mn; Na and B; Cu and Mo; but even this is not all "because" nutrition is not a rigid requirement but is itself a function of environment.'

In other words, the significance of foliar nutrient concentration and foliar nutrient balance may be properly interpreted only when the effects of many other environmental factors are understood. Mathematical models are therefore necessary to show how a large number of environmental factors affect growth, as advocated by Gessel (1967) and Gates (1968), by Czarnowski, Humphreys and Gentle (1967) in specific reference to P. radiata, and by Raupach, Boardman and Clarke (1969) through their use of multivariate analysis relating nitrogen and phosphorus foliar levels to growth of the species in South Australia.

Against this background and attitude the present study was conceived as an examination of interrelationships between site, growth and foliar nutrient concentration, with particular emphasis on nitrogen and phosphorus patterns in the tree crown. In this way it was hoped to establish a firmer basis than currently exists for interpreting the meaningfulness of foliar nutrient levels at standard sampling points in tree crowns.

There are three questions which might be asked concerning any nutrient element and the growth of a forest tree species:

(1) its availability per se in the soil through the rotation period, in relation to the changing demand by the forest on the soil;

(2) the environmental factors which affect the ability of the tree to take up the nutrient from the soil e.g., the pattern of moisture supply, and the interaction of the nutrient with other elements; and

(3) the availability of the tree to use and re-use the nutrient once it is taken up by the tree, and the way environmental factors (e.g., nutrient supply, soil moisture regimes, temperature, etc...) influence this re-use.

These three questions reflect the concept that the whole forest ecosystem, from the parent material to some point in the atmosphere, contributes to forest growth. Ideally, the influence of all components of the ecosystem must be studied to understand variations in forest production, both quantitatively and qualitatively, and more specifically to understand the contribution of particular foliar nutrient concentrations to growth. However, in a study necessarily restricted to a brief time period, any exhaustive analysis of foliar nutrient/environment/growth interrelationships was impossible. Rather, it was decided to explore the way in which foliar nitrogen and phosphorus vary with growth (both quantitatively and qualitatively) and the environment. This has been done by examining:

(1) the way stand age, production (site quality) and environment (distinctive soil types) influence foliar nitrogen and phosphorus concentration;

(2) the way environment (soil types) influences tree habit and foliar concentration patterns;

(3) the way production (site quality) affects the pattern of uptake and distribution of nitrogen and phosphorus in tree crowns; and

(4) the way environment influences patterns of nutrient translocation within the tree crown.

The study is therefore exploratory and broadly based. At this stage of our understanding of foliar nutrient/environment/growth interrelationships, such an approach was regarded as essential. The restriction of the study to foliar nitrogen and phosphorus is also logical. It has been demonstrated on many occasions that they are the major and frequently the only nutrient elements limiting growth of Pinus radiata on poor sites throughout southern Australia. Again, both foliar nitrogen and phosphorus and the nitrogen:phosphorus ratio are now being used to interpret nutritional status of the species in plantations (Raupach, 1967; Raupach, Boardman and Clarke, 1969), despite the inadequately understood physiological basis of such use.

The foliar nitrogen and phosphorus concentrations have been measured as follows:

(1) in 1-year or current needles near the apex of the tree;

(2) the vertical gradient in current needles from the crown apex to the crown base; and

(3) the horizontal gradient at one crown level, through the needle-age range.

These three measurements recognise that in most tree species, both needle age and crown position have an influence on foliar nutrient concentration; and that for a given species, variations in environment, nutrient supply and tree vigour may affect the foliar nutrient patterns within that species (Němec, 1940,1947; White, 1954; Will, 1957; Peterson, 1961; Strebel, 1961; Humphreys and Kelly, 1962; Wells and Metz, 1963; Gagnon, 1964; Madgwick, 1964; Forrest, 1969).

In developing a broad perspective of foliar nutrient/environment/growth relationships, it is a useful starting point to examine under controlled conditions how different nutrient regimes affect the dry matter production and habit of P.radiata seedlings. However, effects cannot be directly extrapolated to field conditions (refer Chapter 1).

Chapter 2 describes a study of the effects of site quality, stand age and soil type on the pattern of change in foliar nutrient concentration with increasing needle age. This has been done on sand dune and associated soils in the south-east of South Australia. This study establishes the important point that the soil environment has a greater influence on foliar nutrients and more particularly the nutrient level/needle age gradient than has site quality or stand age per se. The influence of soil on growth and foliar nutrients has been further examined in Chapter 3, where particular emphasis is placed on branching and the distribution of total biomass amongst the various tree components. Many quality characteristics of P.radiata are under strong genetic control (Fielding, 1960, 1967c)and Forrest (1969) has shown the importance of genotype in nutrient accumulation by individual trees. However,

this study demonstrates a strong site influence on the character of P.radiata crowns. Admittedly, site effects on foliar nutrient concentration and gradients may be related to the phenotype expressions, though the mechanism is not understood.

Several studies have been made recently of the nutrient requirements of moderately to highly productive stands of P.radiata (Will, 1964; Ritchie, 1968; Forrest, 1969). Forrest, for example, has established age-patterns of dry matter production and nutrient uptake in a moderately productive stand at Tumut, N.S.W.; and both horizontal and vertical nutrient concentration gradients within the tree crowns on the same site. In this study, patterns of foliage production, foliar nutrient accumulation and distribution have been investigated on a site of low productivity (Chapter 4) and comparisons with comparable data from the Tumut study contribute further to an understanding of the nutrition of low-site quality stands.

In Chapters 2-4, differences between stands in foliar nutrient gradients within crowns, both horizontal and vertical, are demonstrated. These suggest that nutrient translocation within the tree may vary with such factors as nutrient supply, moisture supply and tree vigour generally. Because of the possible importance of this in the interpretation of foliar nutrient concentration, it was necessary to examine in some detail how site influences the translocation of nutrients within the crown of P.radiata. It is generally accepted that recycling of nutrients within the tree and the relative mobility of different nutrient elements affect the tree's effectiveness to maintain growth (Kramer and Kozlowski, 1960). Chapters 5 and 6 are therefore concerned with the internal translocation of nitrogen and phosphorus. In Chapter 5, seasonal variation in needle dry weight and foliar nitrogen and phosphorus (both concentration and total content per needle) are described for trees of varying vigour, while in Chapter 6, seasonal variation of nitrogen and phosphorus concentration are examined on a poor site under various fertiliser treatments.

CHAPTER 1

GROWTH AND HABIT OF P.RADIATA SEEDLINGS AS INFLUENCED BY VARYING SUPPLIES OF N, P, K, Mg and Ca

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1.1 INTRODUCTION

The interaction of NxP in the field (e.g.,Waring, 1962) and in pot trials (e.g.,Travers, 1965) have been amply demonstrated for P.radiata. Again, others have reported interactions between a major element and a minor element such as AlxP (Humphreys and Truman, 1963) and ZnxP (P. Barker, pers.comm.). A possible Ca response in a P.radiata plantation near Moss Vale, N.S.W., has been reported by W. Gentle (pers.comm.)

However, as far as it is known, the interactions of five major nutrients, i.e.,N, P, K, Mg and Ca, have not been studied. And in view of the ecosystem concept outlined previously, this short chapter attempts to sketch the influence of the five elements and to demonstrate the importance of varying nutrient regimes on (1) growth, (2) habit, and (3) foliar N and P nutrition of P.radiata seedlings in a glass house pot trial.

1.2 MATERIALS AND METHODS

1.2.1 Materials

Seed of P.radiata was obtained from the Tallaganda Seed Orchard in N.S.W. to ensure a high level of genetic uniformity. This was further enhanced by selection in terms of initial seed weight and time of germination (Sweet and Waring, 1966). Surplus seedlings were raised per pot to permit a subsequent selection of the most vigorous seedlings before nutrient solutions were applied three weeks after germination.

The growth medium was a mixture of 50 per cent perlite and 50 per cent vermiculite (Hewitt, 1966).

1.2.2 Experimental design

The experiment used a factorial design N_2x P_2x K_2x Mg_2x Ca_2. However, it was considered that higher orders of interaction than the first order would not be important and would be difficult to interpret. It was also necessary to restrict the size of the experiment. Consequently only 16 rather than 32 treatment combinations were used, viz.,

(For each combination given, the supply of the other nutrient elements was at the lower (1) level)

1	N_2Mg_2	K_2Ca_2	$N_2P_2K_2Mg_2$
N_2P_2	P_2K_2	K_2Mg_2	$N_2P_2Ca_2Mg_2$
N_2K_2	P_2Ca_2	Ca_2Mg_2	$N_2K_2Ca_2Mg_2$
N_2Ca_2	P_2Mg_2	$N_2P_2K_2Ca_2$	$P_2K_2Ca_2Mg_2$

(Reference: Peng, 1967).

Four replicates of each treatment were used, making a total of 64 pots with one seedling per pot. The concentrations of the nutrients were as follows:

Nutrient Level	N	P	K	Mg	Ca
			in ppm		
1	20	6	10	5	20
2	400	100	200	200	1000

Sources of the nutrients were NH_4NO_3, NaH_2PO_4, KCl, $CaCl_2$ and $MgSO_4$. The levels of micronutrients were as follows:

Fe(EDTA)	Mn	Cu	Zn	B	Mn
	in ppm				
5	0.5	0.02	0.05	0.5	0.011

The pH of all solutions was adjusted with HCl and NaOH to the range 5.5-6.0.

The lower levels of the five major nutrients were chosen to provide an adequate nutrient supply as estimated from the literature. The higher levels were not excessive except perhaps Ca_2 at 1000 ppm.

1.2.3 Harvesting and measurement

The experiment was commenced on 15 August 1968 and harvested on 15 September 1969. This lengthy period of 13 months was necessary to permit the full expression of variation in seedling habit. The pot volume used was about 3 litres, and at harvest the largest plants were just becoming root bound. Each seedling was measured for total height, diameter of stem at crown base (cotyledonary scar), number of branches per seedling, fascicle weight and length, total dry weight, and foliar N and P concentration. The results were analysed by computer.

1.3 RESULTS

The responses to the 16 treatment combinations are summarised in Tables 1.1 and 1.2. The results will be presented in three parts, namely, the effect of nutrient treatments on:

(1) total dry weight;
(2) N and P foliar concentrations and N:P ratio;
(3) habit of seedlings.

1.3.1 Total dry weight

(a) NxP interaction

The significance of the NxP interaction can be seen in the following summary:

Combinations of N and P	Range of dry weight (gm)
N_1P_1	6-10
N_1P_2	6-8
N_2P_1	16-34.5
N_2P_2	43-85

Table 1.1

Effect of nutrient combinations on various parameters of *P.radiata* seedlings

Treatment Combinations No.	Treatment (1)	Dry wt. (2)	Foliar N%	Foliar P%	N/P	Ht/Diam (3)	Branch No.	Fas. length (4)	Fas. wt. (4)
1		6.2	1.27	.185	7.0	54.9	7.8	10.1	35
2	N2,P2	63.3	2.99	.514	5.8	49.5	18.0	10.1	41
3	N2,K2	30.1	2.59	.096	26.9	61.4	18.5	10.9	39
4	N2,Ca2	16.2	2.39	.098	25.4	42.2	18.3	7.6	25
5	N2,Mg2	34.5	3.05	.099	30.8	70.8	21.0	8.8	30
6	P2,K2	7.7	1.34	.965	1.4	64.4	9.8	10.3	28
7	P2,Ca2	7.9	1.44	.703	2.2	53.4	9.0	12.0	44
8	P2,Mg2	7.4	1.36	.758	1.9	62.7	11.3	10.3	33
9	K2,Ca2	6.3	1.36	.151	9.2	65.0	11.8	9.4	33
10	K2,Mg2	6.7	1.50	.189	8.0	78.9	6.5	10.8	31
11	Ca2,Mg2	10.1	1.13	.135	8.4	67.8	13.0	12.5	47
12	N2,P2,K2,Ca2	48.5	2.47	.354	7.0	65.5	20.0	13.3	53
13	N2,P2,K2,Mg2	85.4	2.39	.331	7.3	72.8	26.0	11.7	68
14	N2,P2,Ca2,Mg2	42.9	2.27	.346	6.7	57.2	15.5	13.8	59
15	N2,K2,Ca2,Mg2	15.9	2.04	.098	22.1	58.2	13.0	12.5	60
16	P2,K2,Ca2,Mg2	6.0	1.35	.658	2.1	69.2	8.0	11.0	33
L.S.D.($p<0.05$)		5.2	0.43	0.128	4.1	12.8	4.6	0.9	6.6
($p<0.01$)		7.0	0.58	0.171	5.4	17.1	6.1	1.2	8.0

1 = Each treatment combination involved five nutrient elements. Only those elements at the higher level of supply are given. Supply of the others was at the lower level.

2 = Dry weight of aerial part only (gm)

3 = Diameter measured at root collar and height from root collar to tip of plant

4 = Fascicles produced on the internode just below the terminal whorl. Length in cm and weight in mg.

Table 1.2

Significance of nutrient interactions on various parameters of P.radiata seedlings

Nutrient interactions	Dry weight	Fol. N Conc.	Fol. P Conc.	N/P Ratio	Ht/Diam.Ratio	No. Branches	Fascicle length	Fascicle wt.
N x P	xx	—	xx	xx	—	—	xx	—
N x K	xx	xx	—	—	—	—	xx	xx
N x Ca	xx	xx	xx	xx	x	xx	x	xx
N x Mg	xx	xx	xx	—	—	—	x	xx
P x K	xx	—	—	—	—	x	xx	xx
P x Ca	xx	—	xx	—	—	x	xx	xx
P x Mg	xx	—	xx	—	—	—	x	xx
K x Ca	xx	—	xx	—	—	—	—	—
K x Mg	—	—	—	—	—	—	x	xx
Ca x Mg	xx	—	xx	—	—	xx	—	xx

where xx = significant at $p<.01$

x = significant at $p<.05$

— = non significant

Irrespective of the supply of the other three nutrients, an increase in N supply in the presence of low P (P_1) gave a variable though significant increase in dry weight production i.e., from 6-10 to 16-34.5 gm. However, with an increase in P in the presence of low N (N_1), negligible gain in dry weight occurred. When both N and P were at higher levels (N_2P_2) again irrespective of the supply of other nutrients, dry weight increased to within the range 43-85 gm. The interaction of NxP was particularly strong.

(b) Effect of varying K, Mg and Ca

The effect of N and P was so dominant that with an increase in supply of all three nutrients in the presence of low N and P (N_1P_1), there was little gain in dry weight, viz.,

N_1P_1	-	$K_1Mg_1Ca_1$	6 gm
"	-	$K_2Mg_2Ca_1$	7
"	-	$K_2Mg_1Ca_2$	6
"	-	$K_1Mg_2Ca_2$	10

However at higher N and P (N_2P_2), an increase in supply of K, Mg and Ca changed significantly the dry weight production as follows:

N_2P_2	-	$K_1Mg_1Ca_1$	63 gm
"	-	$K_2Mg_2Ca_1$	85
"	-	$K_2Mg_1Ca_2$	48.5
"	-	$K_1Mg_2Ca_2$	43

Increasing the supply of K and Mg (but not Ca) increased the dry weight production to a peak 85 gm per pot for the experiment; but increasing the supplies of K and Ca (and not Mg) and Mg and Ca (and not K) decreased dry weight production to

48.5 and 43 gm per pot respectively. These results show that the balance between the supplies of K, Mg and Ca rather than their absolute levels can critically affect production of P.radiata seedlings when N and P are in adequate supply. In particular it is possible that where the Ca:Mg supply ratio is high, growth is depressed.

Table 1.2 indicates that an interaction of all nutrient combinations (except KxMg) affects dry weight production.

1.3.2 Foliar N and P concentration

Variations in N and P supply had a marked effect on foliar N and P levels as follows:

N and P treatments	Range of foliar nutrient content (%)	
	N	P
N_2P_2	2.27 - 2.99	0.346 - 0.514
N_2P_1	2.05 - 3.05	0.096 - 0.099
N_1P_2	1.34 - 1.44	0.658 - 0.965
N_1P_1	1.13 - 1.50	0.135 - 0.185

Foliar phosphorus concentration was particularly large at the N_1P_2 level of supply, being greater than in the N_2P_2 treatment; that is, where growth is severely restricted by limiting N, phosphorus is taken up in "luxury" quantity (0.658 - 0.965 per cent). However, the reverse is not true of nitrogen: the foliar N concentration in response to the greater N_2 supply and the lower P_1 supply (N_2P_1) was no greater than that of the N_2P_2 treatment (2.27-2.99 per cent). The N supply of nitrogen was evidently more limiting than the P supply of phosphorus.

Good seedling growth requires both an adequate concentration and an appropriate balance of N and P in the foliage. Best seedling dry weight production was in response to the N_2P_2

treatment (48.5, 42.9, 63.3, 85.4 gm per pot for the four treatments) which resulted in a N:P foliar ratio of 5.8 to 7.3.

Intermediate dry weight production was in response to the N_2P_1 treatments for which the foliar N:P ratios ranged from 22 to 31. Lowest production occurred with N:P ratios in the well-balanced range 6.3-7.9, but here foliar concentration of both N and P was low (N_1P_1 treatments). Where the N:P ratios were only 1 to 2 (N_1P_2 treatments), dry weight production was similarly very poor (6-7 gm per pot).

Foliar N and P concentrations have not been markedly affected by varying supply of K, Mg and Ca. An example showing the influence of K is given below:

Treatment	Foliar N concentration (%)
$N_2P_2 - K_1$	2.77 - 2.99
$N_2P_2 - K_2$	2.39 - 2.47
$N_1P_1 - K_1$	1.13 - 1.27
$N_1P_1 - K_2$	1.36 - 1.50
$N_2P_1 - K_1$	2.39 - 3.05
$N_2P_1 - K_2$	2.04 - 2.59
$N_1P_2 - K_1$	1.36 - 1.44
$N_1P_2 - K_2$	1.34 - 1.35

Nevertheless, the following statistical interactions have been shown to influence foliar N: NxK, NxCa, NxMg; and the following to influence foliar P: NxCa, NxMg, PxCa, PxMg, KxCa, CaxMg. Because of statistical complexity, it is difficult to demonstrate these interactions in absolute terms.

In the example with K, increasing supply of K from K_1 to K_2 reduced foliar N slightly when the N supply was at the higher N_2 level; when the N supply was at the limiting N_1 level,

increasing K supply either increased foliar N (N_1P_1) or had little effect (N_1P_2).

Apart from the NxP interaction, the only nutrient interaction statistically affecting the N:P ratios was that of NxCa. At N_2 supply, for example, increase in Ca supply from Ca_1 to Ca_2 may have helped reduce slightly the wide N:P range. For example, it was 30.8 for the $N_2P_1Ca_1K_1Mg_2$ treatment, and 25.4 for the $N_2P_1Ca_2K_1Mg_1$ treatment, although this effect may well be related to the effect of varying the Ca:Mg supply ratio.

1.3.3 Habit of seedlings

The effect of nutrient supply and nutrient interactions on seedling habit were examined in terms of response in:

(a) height:diameter ratio

(b) total number of branches

and (c) fascicle weight and length.

Results are given in Table 1.1 and Table 1.2.

(a) Height:diameter ratio

The only interaction significantly affecting the ratio was that of NxCa. At the lower supply of all nutrients ($N_1P_1K_1Ca_1Mg_1$) the ratio was 54.9. An increase in K,Mg and Ca increased the ratio within the range 65-79; it was greatest (79) where the Ca:Mg supply ratio was low ($N_1P_1K_2Mg_2Ca_1$). At the greater supply of N and P (N_2P_2) increasing Ca, Mg and K supply raised the height:diameter ratio from 49.5 to within the range 57-74. Again at the upper point of the range (73.9) the Ca:Mg supply ratio was low ($N_2P_2K_2Mg_2Ca_1$) i.e.,the better the nutrient balance as far as growth is concerned (see Section 1.3.1), the greater is the height:diameter ratio.

(b) Total branch number per seedling

In broad divisions, the greater the dry weight the larger the number of branches a seedling has. However, within these broad divisions, treatments with a range of dry weight production may have a similar number of branches. For example,

treatments 2-4 in Table 1.1 have a range in dry weight of 16-63 gm per pot, but a similar number of branches (18-21)

Treatment	Dry weight	Total branch number
M_2P_2	63 gm	18
M_2K_2	30	18.5
M_2Ca_2	16	18
M_2Mg_2	34.5	21

Conversely treatments with similar dry weight production may have significantly different numbers of branches e.g.;

Treatment	Dry weight	Total branch number
$N_2P_2 - K_2Ca_2Mg_1$	48.5 gm	20
$N_2P_2 - K_1Ca_2Mg_2$	43	15.5
$N_1P_1 - K_2Mg_1Ca_2$	6	12
$N_1P_1 - K_2Mg_2Ca_1$	7	6.5

Dry weight production was very low in all treatments involving N and P at the lower supply level (N_1P_1), but variation in supply of K, Mg and Ca significantly affected the branch production. Similarly, at the larger N and P supply (N_2P_2), variations in K, Mg and Ca affected total branch number. The following interactions affected branch number at the $P < 0.01$ level of significance: NxCa, and CaxMg.

(c) Fascicle weight and length

There was no definite relationship between fascicle length and total dry weight production. This is possibly because

P supply has a stronger effect on fascicle length than has N supply, as follows:

Treatment	Range of fascicle length
N_2P_2	10 - 14 cm
N_2P_1	8 - 12.5
N_1P_2	10 - 12
N_1P_1	9 - 12.5

At the N_2 supply level, increasing P supply raised the range of fascicle length at the N_1 supply level whereas raising P had little effect on fascicle length. Conversely, at both P_1 and P_2 supply respectively, increasing N supply had no effect on the fascicle length range.

Again, raising K, Ca and Mg supply affected fascicle length at a constant supply of N and P. For example, at the N_2P_2 supply levels, fascicle length was 10.1 cm where Ca, Mg and K were all at the lower level. The length range was 11.7-13.8 with various combinations of K, Ca and Mg at higher levels of supply.

There was no definite relationship between fascicle weight, fascicle length and total dry weight. The effects on fascicle weight of varying N and P were similar to those on fascicle length; and an increase in supply of K, Mg and Ca also tended to increase the fascicle weight.

1.4 DISCUSSION

The effects of fertilisers on phenology and morphology have been stressed by many authors (e.g.,Beaton, Kossick and Speer, 1964; Heiberg, Madgwick and Leaf, 1964; Pineau, 1968). Nitrogen and phosphorus fertilisers increased the size of current needles of Pinus pinaster, their photosynthetic ability, their content of chlorophyll 'a' and 'b', and moisture content (Keay, Turton and Campbell, 1968). The morphology of eucalypts may also vary with variation of nutrient supply. For example, Will (1961)

obtained, for Eucalyptus seedlings, few or no branches with N and P deficient seedlings, but more extensive than normal branching with K-deficient seedlings.

The pot trial for P.radiata described in this chapter had shown that all five major nutrient elements i.e., N, P, K, Mg and Ca, interacted significantly, at least in the first order of interaction, to influence dry weight production, habit, and foliar N and P levels of the seedlings.

While these results cannot be extrapolated directly to the field, they show that any complete interpretation of differences between P.radiata stands in growth, taper, branch production and foliage characteristics can be made only in terms of variation of all factors of the environment. However, there is little doubt that variation in nitrogen and phosphorus supply dominates growth response on most sites in Australia. Therefore, due to the necessary time involved, the nutrient component of this study of site/growth/tree characteristics/foliar nutrients relationships, is restricted to an examination of the levels and dynamics of nitrogen and phosphorus in as many situations as possible, rather than a more exhaustive study of foliar nutrients in a limited situation.

1.5 SUMMARY

A pot trial for Pinus radiata seedlings was conducted in a glasshouse for 13 months, involving a confounded factorial design with five nutrient elements, and each at two levels of supply, i.e., $N_2xP_2xK_2xMg_2xCa_2$.

The results are that all five major nutrient elements interacted significantly, at least in the first order of interaction, to influence (1) dry weight production, (2) foliar N and P, and (3) habit of the seedlings.

All parameters of seedling habit, namely, height: diameter ratio, total branch number, and fascicle weight and length, were significantly affected by the treatments. Seedlings of similar dry weight production had significantly different numbers of branches, and conversely seedlings with a range in

dry weight production had similar numbers of branches.

The experiment emphasises the need to study variations in growth of Pinus radiata in terms of as many factors as possible. Although the NxP interaction dominates the growth of the species, other nutrients also significantly affect growth, both quantitatively and qualitatively.

CHAPTER 2

EFFECT OF SITE QUALITY, STAND AGE AND SUPPORTING SOIL ON FOLIAR NITROGEN AND PHOSPHORUS CONCENTRATION IN SOUTH AUSTRALIAN PLANTATIONS

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2.1 INTRODUCTION

Forest yield, in both quantitative and qualitative terms, is the result of many interacting factors of the environment. It cannot be expected, therefore, that straightforward relationships will exist between wood yield and concentration of nutrients in the foliage. A tree's root system can ramify quickly through a large soil volume, and thereby compensate for a low concentration of essential nutrients in the soil; and an optimum soil moisture regime may compensate for low levels of foliage nutrients. Consequently, similar levels of wood production are achieved on sites varying in soil depth, in nutrient status and in water supply. The elucidation of relationships between forest production and foliar nutrient concentration, and particularly the way these relationships are influenced by soil environment and stand age, seemed the logical first step in obtaining a better appreciation of the role of nitrogen and phosphorus in the nutrition and growth of P.radiata.

An exploratory examination of foliar nitrogen and phosphorus was made in winter 1967 in 16 stands of 0.1 acre in plantations of the Australian Capital Territory (A.C.T.); the plots were of the same age (10 years), but covered a soil type and site quality range. The results are summarised in Table 2.1.

Foliar N concentration generally decreases with decreasing site quality at all locations. But for two exceptions, differences are not significant. By contrast, the influence of site quality on foliar phosphorus concentration is more marked; at four of the six locations, significant differences in foliar phosphorus concentration were recorded.

Foliar N concentration on the shale-derived soil (Plots 1-3) and on one series of granite-derived soil (Plots 6-7) are greater than those at all other locations; moreover, foliar N concentration is maintained at a fairly high level on lower site quality plots on the shale- and the granite-derived soils (Plots 6-7). In this series of stands, therefore, foliar N cannot be directly related to site quality.

TABLE 2.1

Concentrations of Foliar Nitrogen and Phosphorus per cent of P. Radiata Needles in the A.C.T. Sites

Plot No.	Soil parent materials	Rainfall (approx. in)	Age (yrs)	N per cent mean of 8 trees x	N per cent t. test xx	P per cent mean of 8 trees x	P per cent t. test xx
xxx							
1	shale	30	10	1.59	N.S.	0.130	N.S.
2				1.47	N.S.	0.121	N.S.
3				1.46		0.120	
4	mixed sediments	25	10	1.32	N.S.	0.129	N.S.
5	and acid rocks			1.22		0.147	
6	Granitic	30	10	1.67	N.S.	0.191	P<0.01
7	rocks			1.45		0.121	
8	Undifferentiated	30	10	1.33	N.S.	0.169	N.S.
9	granite			1.45	P<0.01	0.160	P<0.01
10				1.11		0.115	
11	Granitic	25	10	1.26		0.132	N.S.
12	rocks			1.15	P<0.05	0.117	N.S.
13				1.28		0.105	P<0.02
14	Granitic	25	11	1.37	N.S.	0.188	P<0.02
15	rocks			1.26	N.S.	0.148	P<0.01
				1.17	P<0.01	0.097	

x At each location the plots are in order of decreasing productivity, as measured by plot predominant height ; successive plots differ by 3-4 ft in predominant height at each location. (In this exploratory investigation on young stands, no attempt was made to classify all 16 plots on a single production scale).

xx Each foliar level is the mean for 8 trees, on a 0.1 acre plot with an approximate spacing of 8 x 8 ft; one branch on the northern side of the crown, on the first lateral whorl, was sampled in July 1967. This means only current needles were sampled.

xxx t - tests between consecutive plots of decreasing productivity were made; where there are three plots, the lower site quality plot has been compared with the higher site quality plot if necessary.

Foliar phosphorus concentration is surprisingly low at two locations - the shale plots (1 and 3) and the mixed parent material plots (4 and 5). On all soils derived from granite parent materials, the foliar P gradient with site quality is steep e.g., from 0.191 to 0.121 per cent (Plots 6-7), from 0.169 to 0.115 (Plots 8-10), and from 0.188 to 0.097 (Plots 14-16). Within this one parent material, site quality may be related to foliar P but the relationship cannot be extended across a distinctive soil boundary.

It is possible that small differences in rainfall at the various locations might have had some influence on foliar nutrient levels. For example, the N-concentration on plots receiving 30 in. is better than that on plots receiving 25 in. but again this may be related to factors other than rainfall. There is no evidence of any rainfall effect on foliar P.

From this exploratory investigation it was concluded that relationships between foliar N and P, site quality and environmental factors might be complex, and a more extensive investigation was needed to demonstrate foliar N and P/site quality/soil type/stand age relationships. It was impossible to make such an investigation in A.C.T. forests. Because the total plantation area is relatively small (28,000 acres in 1969 for P.radiata), the site quality range is narrow, and a given soil type is associated with only a narrow range of stand age, it was not possible to locate a set of stands covering a prescribed range of site quality, stand age, and soil type and with a relatively uniform rainfall regime. By contrast, the plantation area of P.radiata in the south east of South Australia is very much greater (circa 136,000 acres in 1968) and there are a number of distinctive soil types. Site quality range is wide, and plantations are available covering an age range up to 60 years. With the co-operation of the Woods and Forests Department in South Australia, a study of the influence of environment and age on foliar nutrient levels was made in this region.

The study of foliar nutrients in plantations of South Australia is also relevant to the problem of maintaining long-term productivity in these plantations. Second rotation forests have been established for over 30 years, and evidence of a

decline in wood production amounting to an average 25 per cent of first rotation production has been established (Keeves, 1966). There are many factors which could contribute to this (Florence, 1967), but so far, there has been no clear indication of whether the problem is directly related to exhaustion of soil nutrients, blockage in the organic matter decomposition and nutrient release cycle, or to factors involving accumulation of toxic substances or antagonistic organisms. There have been a number of examinations of foliar nutrients in the plantations of South Australia (e.g., Raupach, 1967a), but as far as is known, no attempt has been made to show how these nutrient levels vary with site quality, stand age, and with soil type. It seemed therefore that this study could contribute to elucidating problems of declining production, and is in fact complimentary to an examination of organic matter decomposition and nutrient release being made in the region (Florence, 1968).

Foliar analyses of needles, taken from standard tree positions at a standard time of the year have provided indices of tree nutrient status now widely used in plantation management (Will, 1957; Raupach and Hall, 1963; Richards and Cameron, 1964; Raupach, 1967a and b; Gentle and Humphreys, 1967; Richards and Bevege, 1969). These studies have been directed mainly to defining a particular foliar nutrient concentration known as the limiting or critical level below which growth is affected by an inadequacy or deficiency of that nutrient. The present study is not directly related to this critical level; rather it seeks to show how foliar nutrient levels vary in response to age and environment in stands where growth is apparently unaffected by a deficient nutrient supply.

2.2 MATERIALS AND METHODS

2.2.1 The study region

General climatic data for the region are described in Appendix I. In the south east of South Australia, plantation forests are associated with a more or less parallel series of sand dunes. The dunes are a mantle of aeolian sand deposited over Miocene limestone and calcareous cemented sands. The

podzolised sands are acid, deep, poor in nutrients, and have a low water-holding capacity. There is a very wide range in plantation productivity (Table 2.2) and this is broadly related to depth to clay or the water-retaining layer. For example, satisfactory growth can be predicted where clay is less than 5 feet from the surface; where depth is between 5 feet and 9 feet, growth is regarded as potentially marginal and other parameters of site (e.g., Eucalyptus species, topography) are used as guides; and where the clay layer is more than 9 feet from the surface, the soil is generally regarded as useless for planting.

The Mt. Burr, Nangwarry and Caroline Sands are the principal members of their respective complexes of podzolised sands associated with the aeolian sands of the ranges. Despite their similar mode of formation, these soils are not morphologically identical (Stephens, Crocker and Butler, 1941). In the clay horizon there are marked differences in colour, depth, texture and structure; and the sands of the eluvial horizon differ in mechanical composition. For example, particle size distributions suggest there have been at least two periods or phases during which the sand dunes from which the Nangwarry Sand is fabricated have been subject to re-sorting, and on close inspection the Nangwarry sand is seen to differ from the Mt. Burr sand.

Both the Nangwarry and Mt. Burr Sands have a low to very low content of total phosphorus, typical surface soils containing around 30 and 110 ppm respectively (Table 2.3). Ruiter (1964) has correlated site index of P.radiata growing on these soils with the total amounts of nitrogen and phosphorus in the upper two feet of the soil profile. The greater the depth to clay, the less water is stored at levels accessible to the main root systems in stress periods, and the more intense has been the leaching of nutrients from upper soil horizons.

Within the sand complexes associated with the sand ranges, various humic and meadow podzols occur on lower sites - for example Riddoch Sand, Short Sand, Kalangadoo Sand. These

Table 2.2

Examples of soil type and site quality correlations in South Australia*

Soil Types	Typical depth of clay (ft)	Predominant S.Q. carried by the soil type								
		I	II	III	IV	V	VI	VII	Pinus Pinaster	Unsuitable
Podsolized dune sands										
Mt. Burr Sand										
Shallow phase	To 5	xxxxxxxxxxxx								
Marginal phase	5 - 7			xxxxxxxxxxxxxxxxxxxxxxxxxxx						
Deep phase	7+			xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx						
Transitional MBS-YS	12					xxxxxxxxxxxxxxxxxxxxxxxxxxx			xxxxxxxxxxxxx	
Young Sand	12					xxxxxxxxxxxxxxxxxxxxxxxxxxx			xxxxxxxxxxxxx	
Riddoch Sand	To 3	xxxxxxx								
Tantanoola Flinty Sand	To 3	xxxxxxx								
Loamy phase	To 3			xxxxxxx						
Wandilo Sand	To 3		xxxxxx							
Swampy phase	To 3								xxxxxxxxxxxxxxx	
Sandy swamp soils	1+								xxxxxxxxxxxxxxx	
Short sand	To 2½								xxxxxxxxxxxxxxx	
Terra rossa soils										
Hindmarsh sandy loam	To 2½			xxxxxxxxxxxxxxx					xxxxxxxxxxxxxxx	
Transitionals	To 5			xxxxxxxxxxxx						
TR - M.B.S.										
Transitional basaltic soils										
Sands to sandy loams	2½ +			xxxxxxxxx						

xxxxxxxx Main occurrences
———— Exceptional occurrences

* Lewis and Harding (1963)

Table 2.3

Chemical analyses of selected soils within the dune systems in the south east of South Australia (from Stephens et al., 1941)

A. SAND					
	Depth (in)	0-6	6-13	13-42	42-60
Mt Burr Sand	P_2O_5 (ppm)*	110	70	-	300
	N per cent	0.044	0.121	0.008	
	Depth (in)	0-5	5-13		72-96
Nangwarry Sand	P_2O_5 (ppm)	30	20		120
	N per cent	0.043			
	Depth (in)	0-10	10-21	96-114	114-132
Young Sand	P_2O_5 (ppm)	40	20	30	120
	N per cent	0.058	0.017		
B. MEADOW PODZOLIC					
	Depth (in)	0-5	5-12	12-27	27-36
Wandilo Sand	P_2O_5 (ppm)	140	90	110	60
	N per cent	0.119			
C. TERRA ROSSA					
	Depth (in)	0-4	4-17	17-35	
Hindmarsh Sandy Loam	P_2O_5 (ppm)	730	720	750	
	N per cent	0.129	0.063	0.040	
D. SAND WITH LIMESTONE INFLUENCE					
	Depth (in)	0-6	6-18	18-21	21-60
Mt Muir Sand	P_2O_5 (ppm)	200	130	-	270
	N per cent	0.052	0.023		

* Total P - HCl extraction

soils are also very infertile in terms of total phosphorus (HCl-extractable) but where the leached sand is underlain at 2-3 feet by massive limestone-derived clay, production of Pinus radiata may be very good (e.g., Riddoch sand). Alternatively, where an organic hard pan underlies 6 or more feet of light grey or white sand, production may be very poor (e.g., Young Sand).

Within transition zones between the aeolian sands and the flats and plains, meadow and humic podzols occur, with many variations in morphological features, depending largely on the elevation of the site. These form a group known as Wandilo Sand and plantations on them are generally highly productive. The group has been subject to the same soil forming factors as the podzolic sands with the addition of the effect of a fluctuating water table. Up to three feet of dark grey sand and organic-stained sand or hard pan overlie yellow-brown grey clay with red inclusions. Total phosphorus is relatively low (140 ppm), but better than that for most sand profiles (Table 2.3).

Throughout the sand dune system, Terra Rossa soils occur where the underlying limestone has been exposed. These soils are generally shallow but may be moderately fertile. Plantations of P.radiata are typically within the low production range for the species (Table 2.2), and may be subject to severe moisture stress. Drought die-back (autumn-brown top) is common (Milikan and Anderson, 1957).

Although Terra Rossa soils themselves are present over only a small part of the dune system, limestone has influenced much of the soil, producing a wide gradational range between Terra Rossa and sand profiles. This may mean a slight modification only to surface or subsurface sand colour, or alternatively, dark grey-brown sand may grade through yellow brown sand to a bright reddish yellow clay at 2-3 feet. There is a wide range in productivity on the transitional soils and at the upper end of the range stands of SQ II are produced (Table 2.2).

Volcanic extrusions (basalt) have also influenced soils in the dune system although definite influences are localised.

It is possible however that some of the Terra Rossa-Sand transitionals may have some degree of volcanic influence.

Because of the complex mosaic of soil types, and within any one soil type, variations in topography and depth to clay or other water retaining horizon, most South Australian plantations have a complex production mosaic. For management purposes, seven production classes are recognised, viz., site quality I to VII (Lewis, 1954). The production range associated with this site quality range is as follows:

		Predominant height* (ft) at 30 years	Mean annual increment at 30 years (c.ft/ac./yr)
SQ	I	132	400
	II	124	370
	III	117	330
	IV	109	290
	V	101	250
	VI	92	196
	VII	78	130

* In South Australia, volume production is the primary determinant of site quality; predominant height (mean height of tallest 30 trees per acre) may vary somewhat between stands having similar volume production (see Jacobs, 1962).

2.2.2 Sampling method

Thirty-four plantation sites in the south-east of South Australia were selected for foliar sampling. These covered variations in site quality, stand age and soil type. Twenty of the plots were sampled in May 1968 and the remainder in November of the same year. Because of seasonal variation in foliar nutrient concentration, the data for the two samples are considered independently.

At each site, stand predominant height was taken to ensure the sample trees were within the required site quality class. At

each site, eight (or occasionally nine) dominant and co-dominant trees were randomly selected for sampling. Up to about 20 years of age, trees were climbed, and the fourth major annual whorl back from the tip was removed. This branch carried needles over the 1 to 4-year age range. In some stands, the four-year needles had already been shed, especially in the winter sampling. Samples of the 1 to 4-year needles were taken, bagged and labelled separately. For stands older than 20 years, one branch was removed as close as possible to the 4-year whorl, using a .222 rifle fitted with an 8x telescope and charged with high velocity, soft-nosed bullets. It was not always possible to bring down a 4-year branch, particularly in lightly thinned stands, but it was stipulated that only branches in the 4-6 year range were to be sampled and any branch not having recent expansion (May sampling) or not actively expanding (Spring sampling) was to be rejected. The suitability of this method of sampling is considered adequate for the purpose (Tamm, 1964) and compares favourably with the current standard method of foliar sampling in these plantations (e.g., Raupach, 1968). Raupach adopted a standard sampling procedure for South Australia as a result of extensive studies (Raupach, 1967a): needles are sampled in March (i.e., in Autumn) from at least six trees in any location and analysed either separately for each tree or as two composite samples of three trees. They are sampled from within six inches of the tip of a lateral branch one-third of the way down the crown, or preferably, from the second whorl from the tip of the tree provided that it has developed in the current season; otherwise the first whorl is sampled.

A complete list of all 34 sites, showing location, stand age, soil type and site quality, is given in Table 2.4.

2.3 RESULTS

2.3.1 Effect of site quality and stand age on foliar nitrogen and phosphorus concentration

The foliar sampling for this study made in May 1968 covered an age range within each of three site quality classes (SQ V, III and II). Within the SQ V and SQ III series, soil type

Table 2.4

Sample plots in the south east of South Australia

A. May 1968 collection

Site Quality (SQ)	Age (years)	Soil type	Location
SQ II	13	Meadow Podzolic	
	23	Meadow Podzolic	
	32	Sandy Meadow Podzolic	
	32	Nangwarry Sand	Cpt 4 P.F.R.+
	39	Mt Muir Sand Trans	
	47	Nangwarry Sand Trans	Cpt 10 P.F.R.
SQ III	11	Nangwarry Sand	
	23	Nangwarry Sand	P.F.R.
	32	Nangwarry Sand	Cpt 5 P.F.R.
	35	Nangwarry Sand	P.F.R.
	59	Nangwarry Sand	Cpt 10 P.F.R.
SQ V	13	Mt Burr Sand	Snuggery
	21	Mt Burr Sand	
	31	Mt Burr Sand	Logging track Mt Burr
	42	Mt Burr Sand	Logging track Mt Burr

B. May 1969 collection

SQ IV	11	Nangwarry Sand	P.F.R.
	11	Mt Burr Sand	Holloways
	11	Volcanic Soil	Holloways
	11	Terra Rossa	Holloways
SQ VII	11	Nangwarry Sand	P.F.R.

C. November 1968 collection

SQ III	31	Nangwarry Sand (N.S.)	Cpt 4
SQ II	41	Nangwarry Sand	Cpt 57
SQ II	28	Wandilo Sand	Cpt 5
SQ II	27	NS x Wandilo Sand	Cpt 2
SQ II	32	Sandy meadow Podzolic	School plot P.F.R.
SQ II	29	Mt Burr Sand - Strong Colour	Cpt 6
SQ II	29	Mt Burr Sand - Brown phase	Cpt 6
SQ III	28	Mt Burr Sand at Mt Burr	Cpt 18 Mt Burr
SQ II	28	Terra Rossa x Mt Burr Sand	Cpt 19 Mt Burr
SQ II	27	Terra Rossa x Mt Burr Sand	Cpt 6 Tantanoola
SQ V	26	Terra Rossa at Mt Burr	Cpt 8 Mt Burr
SQ IV-V	25	Terra Rossa at Tantanoola	Cpt 4 Tantanoola
SQ II	30	Mt Burr Sand at Tantanoola	Cpt 3 Tantanoola
SQ II	31	Mt Burr Sand with limestone	Cpt 8 Tantanoola

+ P.F.R. = Penola Forest Reserve

was held constant, but within the SQ II series two soil types were included as follows:

SQ	Soil type	Stand age (years)
V	Mt Burr Sand	13
		21
		31
		42
III	Nangwarry Sand	11
		23
		32
		35
		59
II	Meadow Podzolic (Wandilo Sand)	13
	Sandy Meadow Podzolic	23
	Mt Muir Sand	32
	(Terra Rossa x Sand Trans.)	39

Foliar nutrient levels (nitrogen and phosphorus) for the above stands are given in Table 2.5; each figure is the mean of 8 sample trees. Least significant differences (L.S.D.) are given for each of the four needle ages.

(a) Foliar phosphorus

(i) SQ V series (Mt Burr Sand)

In the younger stands (13 and 23 years), very high foliar phosphorus levels were recorded in 1-year needles (Fig. 2.1). Indeed, these levels (0.230 - 0.240 per cent) are higher than those for any other site quality, age or soil. The gradient in needle phosphorus as a function of needle age is steep.

Foliar phosphorus concentration in the stands at ages 31 and 42 is in striking contrast. At 31 years, the foliar P concentration is 0.142 per cent, i.e., just on the concentration

Table 2.5

Influence of site quality and stand age on foliar nutrient levels in *P. radiata*

Soil and S.Q. series	Stand age (years)	N per cent * Needle age (years)				P per cent * Needle age (years)			
		1	2	3	4	1	2	3	4
S.Q. V on	13	1.43	1.25	0.98	1.02	.238	.187	.166	.143
Mt Burr	21	1.39	1.16	1.01	0.95	.232	.181	.166	.151
Sand	31	1.40	1.26	1.20	-	.142	.098	.093	.093
	42	1.29	1.23	1.16	-	.111	.081	.084	.080
S.Q. III	11	1.55	1.40	1.23	-	.134	.126	.120	-
on Nangwarry	23	1.70	1.40	1.37	-	.174	.144	.142	-
Sand	32	1.46	1.20	1.29	-	.159	.128	.120	-
	35	1.22	0.90	0.95	-	.120	.100	.094	-
	59	1.57	1.45	1.37	-	.139	.119	.108	-
S.Q. II Meadow Podzolics	13	1.64	1.59	1.34	1.24	.145	.131	.117	-
	23	1.46	1.35	1.19	1.05	.146	.138	.120	-
Sandy Meadow Podzol	32	1.66	1.59	1.39	-	.167	.127	.127	-
Mt Muir Sand	39	1.64	1.46	1.15	1.07	.187	.161	.132	-
L.S.D. at P < 0.05		0.15	0.13	0.10	0.11	.030	.024	.025	.020

* Each value is the mean of 8 sample trees.

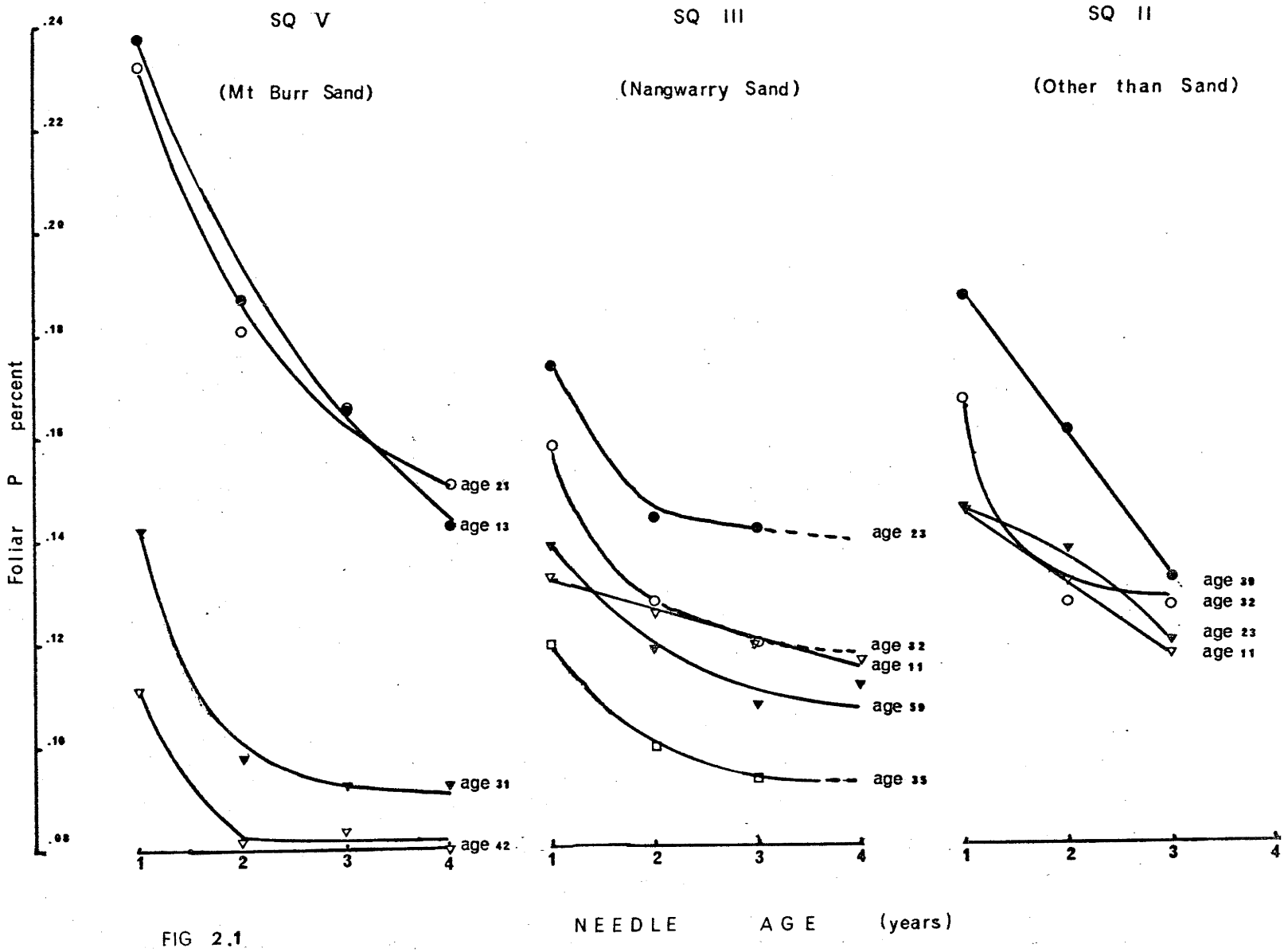

FIG 2.1

Effect of site quality (SQ) and stand age on foliar phosphorus concentration in one to four year needles. (See Table 2.5).

frequently quoted as being the lowest level associated with satisfactory growth (Raupach, 1967a and b). The foliar phosphorus concentration in 1-year needles in the 42-year stand (0.111 per cent) is below this level. For both the 31 and 42-year stands, the gradient in foliar P between 1- and 2-year needles is steep, but thereafter there is no or little further decline.

(ii) SQ III series (Nangwarry Sand)

Foliar phosphorus concentration in SQ III stands growing on the Nangwarry Sand differs from that for the SQ V stands on Mt Burr Sand in a number of ways:

- the younger SQ III stands on Nangwarry Sand (11 and 23 years) do not have the exceptionally high foliar P concentration
- the foliar-P gradient with needle age is not as steep; it is evident that the foliar P gradient between 1- and 2-year needles in all four SQ V stands on Mt Burr Sand is steeper than that for all SQ III stands on Nangwarry Sand
- there is no obvious relationship between foliar-P level and stand age within the SQ III series. Indeed, in a 59-year stand on Nangwarry Sand, foliar-P level is similar to that of a 30-year SQ V stand on Mt Burr Sand. Moreover, the foliar-P gradient with needle age in the 59-year stand is much less steep than that recorded for the 30-year SQ V stand.

There is one Nangwarry Sand stand which might be regarded as atypical. This is the 35-year old stand. It was deliberately included in the sampling because of the narrow crowns of the trees, and the very short and chlorotic needles; moreover, there were no 4-year needles and on many trees there had been considerable shed of 3-year needles. The foliar-P concentration in 1-year needles is only 0.120 per cent, but despite this, the gradient with needle age is similar to that for other healthy stands on Nangwarry Sand.

It is unclear whether such a stand has maintained a

relatively high production over the rotation despite a low foliar-P concentration, or whether soil phosphorus recently became exhausted. If the latter were the case, a steeper needle-age gradient might have been expected because of translocation to new growth.

(iii) SQ II series (Meadow Podzolics and Mt Muir Sand)

This high site quality series has a number of distinctive features. The foliar-P concentration in 1-year needles increases with stand age, that is, the trend contrasts with the steep decline in foliar-P in the SQ V age-series. And with the exception of the 32-year stand, the needle-age gradient is close to a straight line.

It is clearly impossible to make a simple definitive statement concerning a relationship between foliar-P and site quality over the age range. If this is done at say 10 years, using the 1-year needle levels, the SQ V stand has the highest level, the SQ III stand the lowest level, with the SQ II stand intermediate. Alternatively, if 1-year needles in a 30-year stand are compared, the foliar level rises slightly with site quality; and when stands of 40 years and over are compared, there is a strong increase in foliar-P with site quality.

(b) Foliar Nitrogen

(i) SQ V series (Mt Burr Sand)

Between 20 and 30 years, foliar-P levels declined sharply and this rate of decline continued through to 40 years. However, the influence of stand age on foliar nitrogen levels is quite different (Fig. 2.2). Foliar-N in 1-year needles does not decline clearly between 20 and 30 years; indeed it remains constant in stands over the 10-30 year range (about 1.40 per cent) and the difference between these stands and that at 42 years (1.29 per cent) is relatively small. However, there seems to be one difference between the younger and older stands, i.e., the N-concentration gradient with needle age is much steeper at 13 and 21 years than at 31 and 42 years. If the phosphorus patterns are indicative of a considerable phosphorus stress developing after about 20 years within SQ V stands growing on

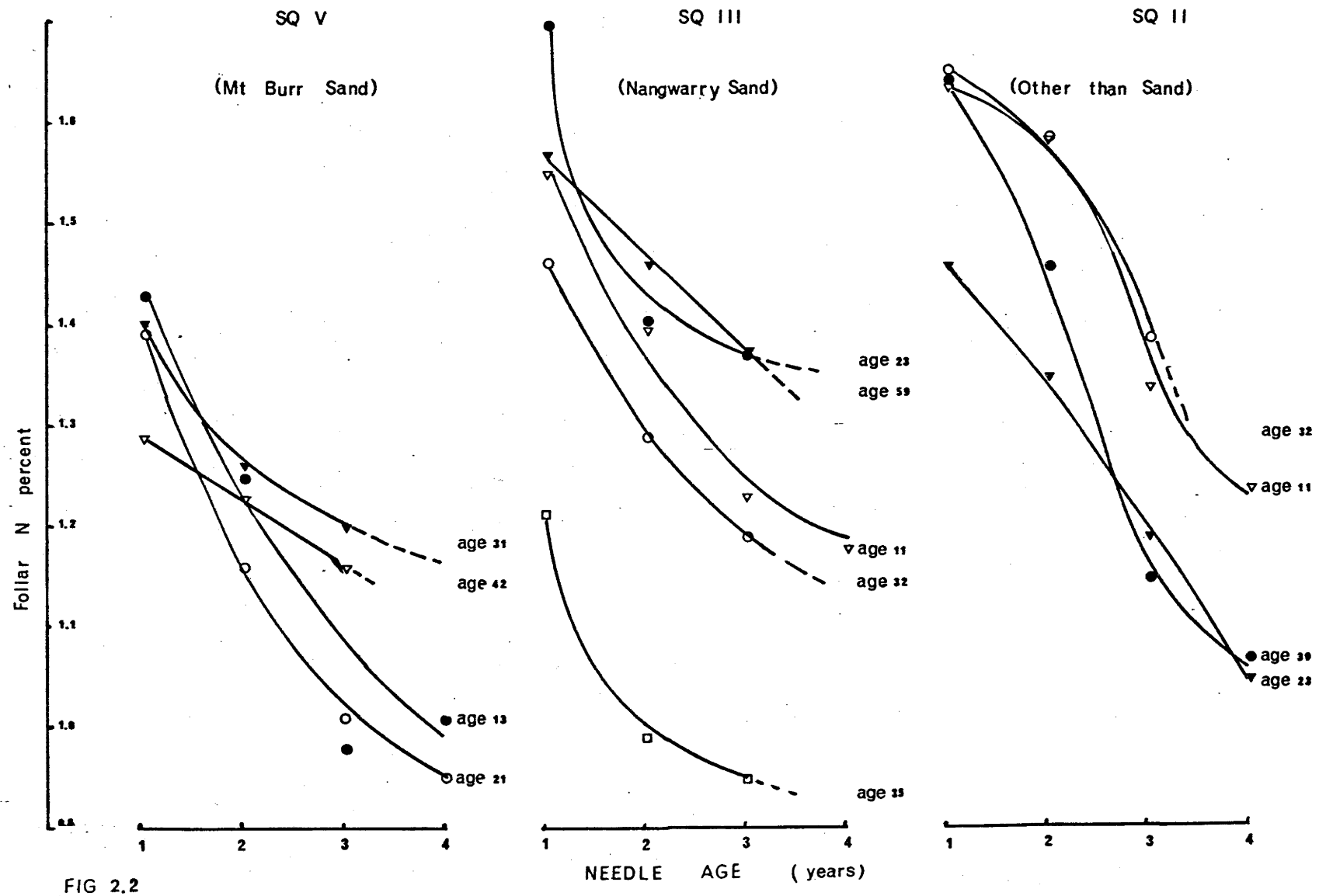

FIG 2.2

Effect of site quality (SQ) and stand age on foliar nitrogen concentration in one to four year needles. (See Table 2.5).

Mt Burr Sand, then the same certainly cannot be said for nitrogen, or at least the stress is not of the same order. The foliar N per cent at 42 years (1.30) is below the suggested lower level for satisfactory growth (i.e., 1.40 per cent), but the needle age gradient is not steep.

(ii) SQ III series (Nangwarry Sand)

With the notable exception of the 35-year stand, foliar-N levels are greater for the SQ III series on Nangwarry Sand than for the SQ V series on Mt Burr Sand.

There is also no clear pattern of variation in foliar-N with stand age; the 23-year stand has a foliar-N concentration in 1-year needles of 1.70 per cent, the 59-year stand 1.57 per cent, the 11-year stand 1.55 per cent and the 32-year stand 1.46 per cent.

(iii) SQ II series (Meadow Podzolics and Mt Muir Sand)

Three of the four stands sampled have foliar-N levels in 1-year needles of around 1.66 per cent; the fourth, the 23-year stand on the Meadow Podzolic has a foliar concentration of 1.46. Therefore, there is no clear pattern of variation in foliar-N with stand age in the SQ II series. The range of foliar-N concentration in these stands is much the same as that in the SQ III series on Nangwarry Sand. The foliar-N gradient with needle age is also similar to that of the SQ III series.

Apart from the lower levels of foliar-N in the SQ V series, nitrogen per cent tends to be much more uniform over the whole site quality and stand age range than foliar-P. Distinctive foliar-N/stand age patterns are not apparent with any site quality class, and the needle age/foliar N gradients are, with few exceptions, more or less parallel. Nitrogen concentration is therefore less sensitive to variations in production and stand age than phosphorus concentration. This supports Waring's view (1964) that the phosphorus content in foliage is useful for diagnostic purposes, but the nitrogen content may not have a similar practical value.

2.3.2 Effect of variation in soil type on foliar nitrogen and phosphorus concentration

Within the site quality range SQ II to SQ V foliar nitrogen and phosphorus may vary both with site quality and stand age. However, as each site quality class in the foregoing study was associated with a different soil type, it seemed possible that the foliar nutrient variations could be related, in part at least, to variations in soil type quite independently of site quality. The influence of soil type on the foliar nutrient levels was unclear. Therefore, it was necessary to examine how soil type affects both foliar nutrient level and the needle age/foliar nutrient gradient. This has been done by examining foliar nitrogen and phosphorus concentration in a series of stands within a narrow site quality and age range, but covering a wide soil type range.

Foliar samplings for this study were carried out in November 1968 and May 1969 respectively.

In November 1968, 14 sites were selected for sampling as follows:

(i) Ten sites were located on areas delimited as SQ II sites on South Australia Woods and Forests Department management maps. Predominant height checks were made at these sites, but as predominant height is only one stand parameter involved in site quality mapping, it is not a precise indicator of site quality class. Nevertheless, the measurements were taken to verify each sampling site was within, or close to, the prescribed site quality II (SQ II).

(ii) Two sites were within site quality class III. These included a stand on Mt Burr Sand and a stand on Nangwarry Sand. The SQ III stand on Mt Burr Sand was included because all 'Mt Burr Sand' soils investigated carrying SQ II stands had stronger surface or subsurface coloration than 'normal' Mt Burr Sand.

(iii) The SQ II stands include a number identified as Mt Burr Sand - Terra Rossa Transitional soils. Therefore for comparative purposes, two low quality stands on

shallow Terra Rossa soil were included in this study; they are SQ IV and SQ V stands respectively.

In May 1969, four eleven-year stands, each SQ IV, were sampled. These stands occur on Mt Burr Sand, a Terra Rossa, and a volcanic-enriched Mt Burr Sand respectively.

A complete list of sites included in this study showing location, stand age, soil type and site quality class is presented in Table 2.4.

Foliar nutrient levels (nitrogen and phosphorus) for stands sampled in November 1968 are given in Table 2.6, and for stands sampled in May 1969 in Table 2.7. In both tables, each value is the mean of eight sample trees. Least significant differences (L.S.D.) are given for each of the four needle ages.

(a) Foliar phosphorus (November 1968 sampling)

The foliar phosphorus data can be considered in three soil categories:

(i) The Sands: these include the two Nangwarry Sand stands, and four Mt Burr Sand stands (including the soil with a stronger sub-surface soil colour than "normal" Mt Burr Sand, and the soil at Tantanoola containing some small pockets of limestone (Table 2.6)).

(ii) The two Meadow Podzolic soils (Wandilo Sand and Sandy Meadow Podzolic) and a soil with varying depth of typical Nangwarry Sand over a Wandilo-type clay, which will be referred to as a Wandilo Sand x Nangwarry Sand transitional.

(iii) All Mt Burr Sand x Terry Rossa transitionals, and the two Terra Rossa soils.

Within each soil category there is considerable variation in per cent phosphorus in 1-year needles, but there is no distinctive difference between the categories (Fig. 2.3). Foliar Phosphorus in the Sand group ranges from 0.117 per cent (mean of three Mt Burr Sand stands) to 0.147 per cent (Nangwarry Sand, SQ III). The range in the Meadow Podzolic group is 0.112 to 0.151 per cent and the range in the Terra Rossas and Sand x Terra Rossa transitionals is 0.112 to 0.151 per cent. This latter range

Table 2.6

Influence of soil type on foliar nutrient levels in P.radiata (November 1968 sampling)

Site Quality (S.Q.)	Soil type	N per cent* Needle age (years)				P per cent* Needle age (years)			
		1	2	3	4	1	2	3	4
III	Nangwarry Sand	1.40	1.24	0.97	0.92	.146	.077	.057	.042
II	Nangwarry Sand	1.53	1.30	1.10	1.03	.130	.085	.078	.065
III	Mt Burr Sand (at Mt Burr)	1.49	1.33	1.34	1.02	.121	.086	.078	.067
II	Mt Burr Sand at Tantanoola	1.64	1.34	1.07	1.00	.111	.076	.057	.044
II	Mt Burr Sand with limestone pockets at Tantanoola	1.82	1.56	1.38	1.10	.147	.087	.072	.068
II	Mt Burr Sand with strong sub-surface colour	1.53	1.41	1.23	1.25	.119	.077	.067	.047
II	Mt Burr Sand (brown surface phase)	1.98	1.73	1.52	1.35	.112	.100	.087	.068
II	Mt Burr Sand x Terra Rossa at Mt Burr	1.67	1.62	1.53	1.29	.151	.126	.011	.100
II	Mt Burr Sand x Terra Rossa at Tantanoola	1.82	1.68	1.49	1.30	.079	.067	.062	.054
II	Wandilo Sand (Meadow Podzolic)	1.63	1,51	1.26	1.18	.113	.085	.087	.079
II	Sandy Meadow Podzolic	1.56	1.33	1.38	1.25	.127	.095	.098	.068
II	Wandilo Sand x Nangwarry Sand	2.03	1.84	1.44	1.16	.129	.119	.089	.065
V	Terra Rossa at Mt Burr	1.56	1.39	1.33	1.27	.122	.095	.082	.061
IV-V	Terra Rossa at Tantanoola	1.50	1.45	1.37	-	.139	.101	.082	-
	L.S.D. ($P<.05$)	0.12	0.11	0.09	0.08	.026	.015	.010	.011

* Each value is the mean of 8 sample trees

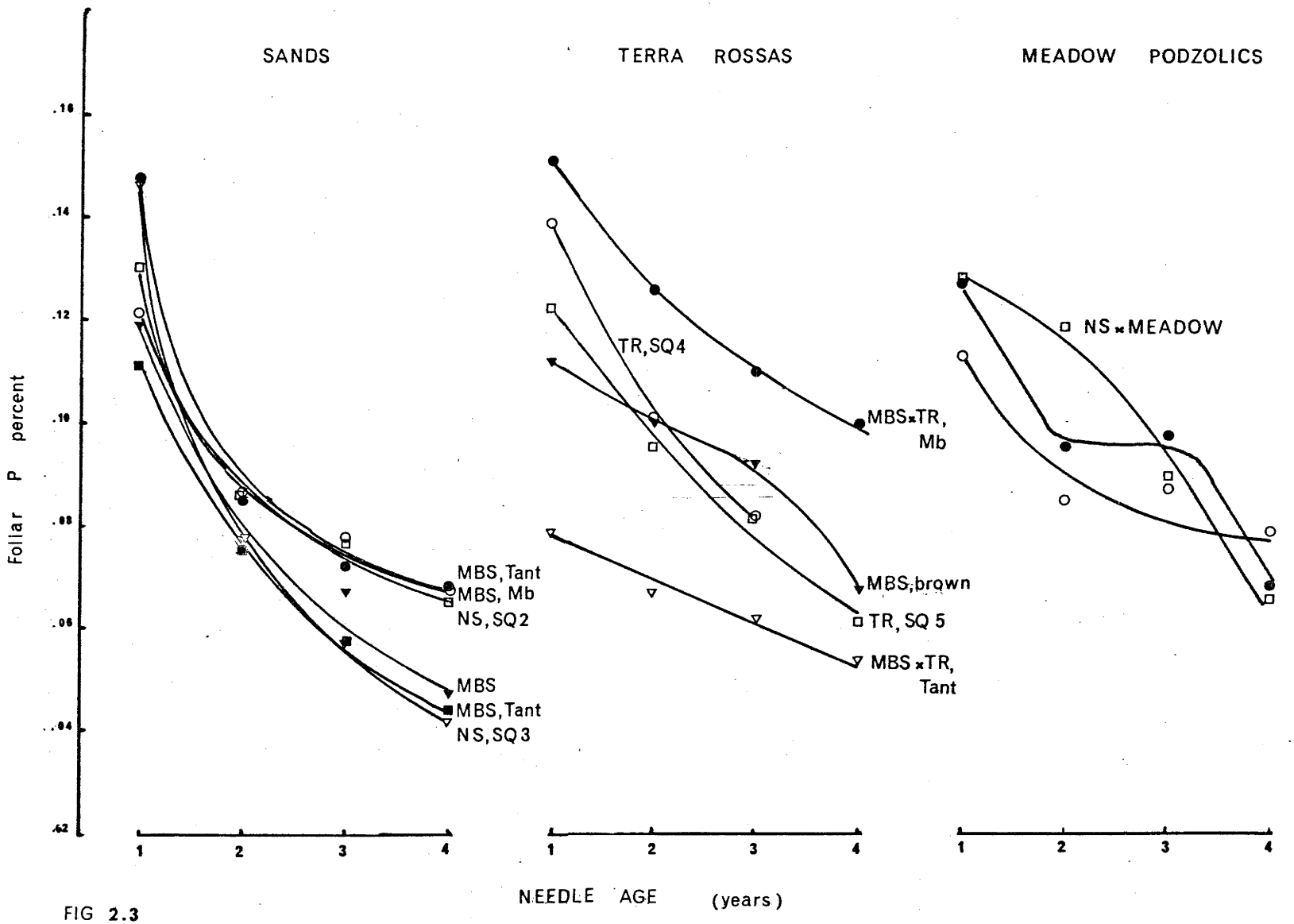

FIG 2.3

Effect of soil type on foliar phosphorus concentration in one to four year needles. (See Table 2.6). All stands are approximately site quality II and about 30 years of age. Soil types: NS = Nangwarry sand, MBS = Mt Burr sand, TR = Terra rossa. Place names: Mb = Mt Burr, Tant = Tantanoola.

excludes the Mt Burr Sand - Terra Rossa transitional at Tantanoola. This has exceptionally low foliar phosphorus (Table 2.6) and the reason is unknown; perhaps it may be related to some extreme seasonal nutrient translocation pattern specific to edaphic conditions or soil moisture at this site.

Foliar phosphorus levels in stands on Mt Burr Sand (0.111, 0.119, 0.121 per cent) are lower than those in stands on Nangwarry Sand (0.130, 0.146 per cent). It is possible, therefore, that low foliar phosphorus concentration of the older SQ V stands on Mt Burr Sand (Fig. 2.2) is as much a function of the particular soil as it is of site quality per se. Again, despite their low site quality, the stands on Terra Rossa soils (SQ IV and SQ V respectively) have foliar phosphorus levels exceeded only by three other stands in the whole soil series.

One of the most striking features of the foliar phosphorus data is the pattern of variation in the needle age/foliar concentration gradient. The gradients are similar within and distinctive for each soil category (Fig. 2.3). All the Sand group gradients are curvilinear and there is a particularly steep gradient between 1 and 2-year needles. Because of this, foliar phosphorus levels in 3 and 4-year needles are low, i.e., below 0.080 per cent for all 3-year needles and below 0.070 for all 4-year needles.

By contrast, the needle age/foliar nutrient gradients for stands on Terra Rossa-Sand transitionals are not curvilinear but are very close to straight lines, irrespective of the foliar concentration in the 1-year needles. Despite the very low foliar phosphorus in the 1-year needles of the transitional soil at Tantanoola, the needle age gradient is similar to that of others in the group. The 1-year to 2-year gradient in this group is much less steep than that shown for the Sand group, and with the exception of the Tantanoola transitional, all foliar phosphorus levels in 3-year needles are greater than 0.080 per cent.

The foliar phosphorus/needle age pattern for the Meadow Podzolic group differs again from that associated with either Sand or Terra Rossa-influenced soils. On both the Sandy Meadow Podzolic and the Meadow Podzolic (Wandilo Sand) soils, the foliar

phosphorus concentration is the same in both 2-year and 3-year needles, and this concentration is greater than 0.080 per cent. In this respect the Meadow Podzolic soils are similar to the Terra Rossa-influenced soils, but distinctly different from the Sand group.

The "Wandilo Sand x Nangwarry Sand transitional" is particularly interesting. The depth of typical Nangwarry Sand to the heavy meadow podzolic type clay horizon is variable, but is as much as eight feet. Qualitatively, this soil carries a very fine stand; tree crowns are larger than on normal Nangwarry Sand sites, but the tree form and branching do not have the coarseness of some other heavy-crowned stands. Apparently the particular type of clay layer present at depth in this soil ensures excellent moisture storage at depths still accessible to the root systems. Despite the fact that foliar phosphorus concentration in 1-year needles is no different from that on typical Nangwarry Sand sites, the Nangwarry Sand x Wandilo Sand transitional maintains a high foliar phosphorus content in 2-year needles (0.119 per cent) and the contrast with Nangwarry Sand (0.077 and 0.085 per cent) is readily evident in Fig. 2.3. The stand on this transitional also differs from stands of similar site quality on Nangwarry Sand in the relatively very small accumulation of litter, despite the apparently greater crown production (Florence, R.G., pers. comm.)

(b) Foliar nitrogen (November 1968 sampling)

When stand age and site quality class are held constant, variation in soil type seems to have a greater effect on the needle age/foliar phosphorus gradient than on phosphorus concentration in 1-year needles. In contrast to this, soil type has a marked influence on the foliar nitrogen concentration over the whole needle age range (Fig. 2.4). Within five of the Sand group stands, foliar nitrogen levels in 1-year needles range from 1.40 to 1.64 per cent. Although in no way a 'transitional', the sixth stand has scattered pockets of decomposing limestone in a Mt Burr Sand profile, and foliar nitrogen concentration on this soil is 1.82 per cent. On Terra Rossa and Terra Rossa transitional soils, the range in foliar nitrogen in 1-year needles is 1.50

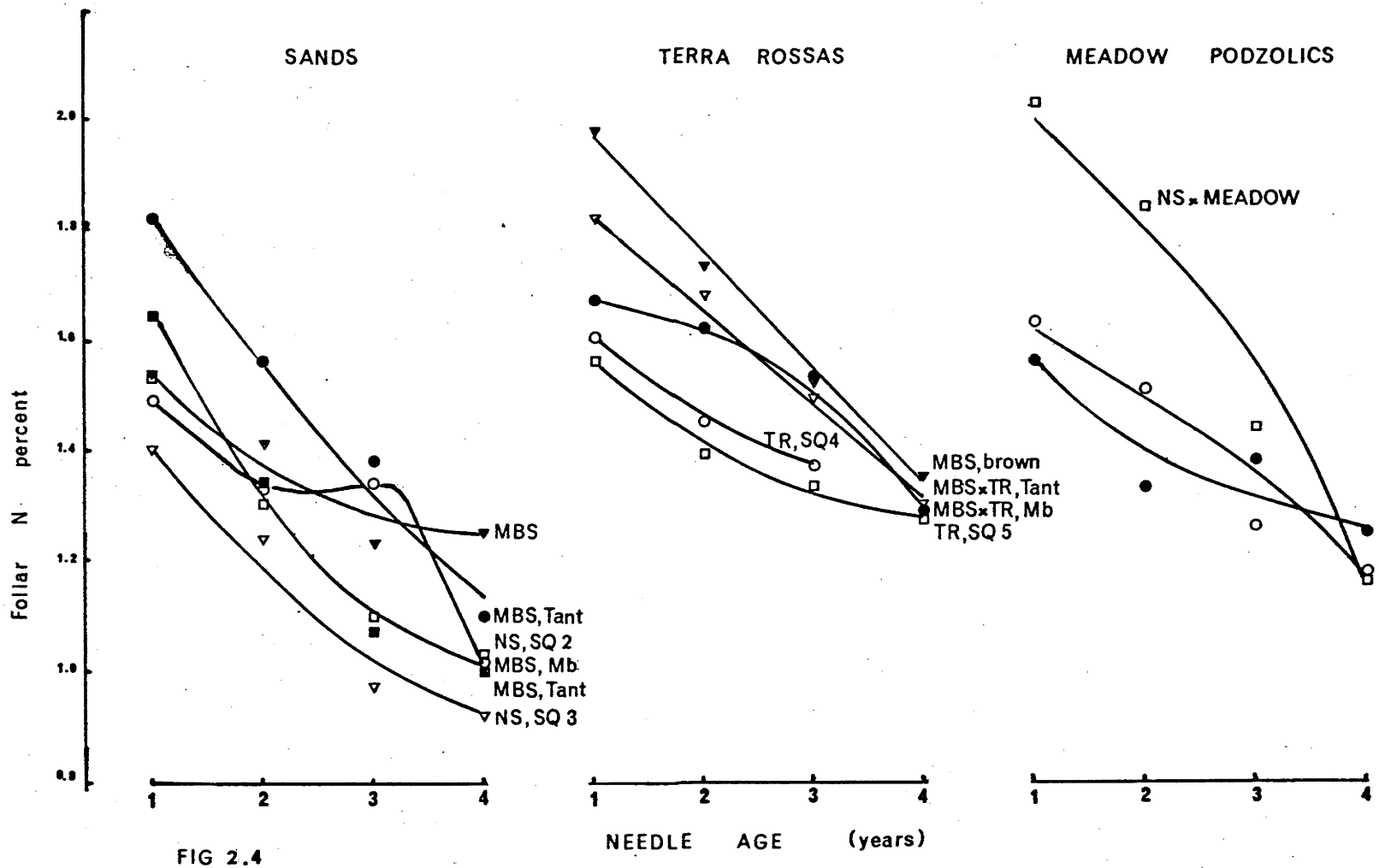

FIG 2.4

Effect of soil type on foliar nitrogen concentration in one to four year needles (see Table 2.6). Details are as for Fig. 2.3.

Despite their low site quality, the two stands on Terra Rossa soil (SQ IV and V respectively) have foliar nitrogen levels (1.50, 1.56 per cent) greater than most of the SQ II and SQ III stands on Mt Burr and Nangwarry Sands. The foliar nitrogen in the stands on Terra Rossa x sand transitionals is even higher i.e., 1.67 to 1.98 per cent. The contrast between the Sand and Terra Rossa-influenced groups is even more striking in the 4-year needles; on the Sands the foliar nitrogen range is 0.92 to 1.25 per cent, and on the Terra Rossa-influenced soils the range is 1.27 to 1.35 per cent.

The two stands on Meadow Podzolic soils have 1-year foliar nitrogen percentages equivalent to those of the upper end of the Sand range, but because the needle age/foliar nitrogen gradients are not as steep, the nitrogen concentration in 4-year needles does not drop to the level of the Sand group.

As in its foliar phosphorus, the Nangwarry Sand x Wandilo transitional has a distinctive nitrogen pattern. The N concentration in the 1-year needles is the highest recorded in the whole soil series; and in fact, the foliar nitrogen per cent in 2-year needles is higher than that recorded in 1-year needles within the Sand group. Thereafter the foliar nitrogen gradient is steeper, and at 4-years the concentration is equivalent to that at the upper end of the Sand range.

(c) Foliar nutrient concentration (May 1969 sampling)

In May 1969, four SQ IV stands 11 years of age were sampled on four different soils. Foliar N and P levels are summarised in Table 2.7 and presented graphically in Fig. 2.5.

(i) Foliar P

The differences in foliar P levels between stands on the four soils are generally similar to those previously described (Fig. 2.3).

Trees on Terra Rossa, Mt Burr Sand and the Volcanic-influenced sands (all SQ IV) have similar P concentrations in 1-year needles (0.176 - 0.179 per cent). By contrast, the Nangwarry Sand (again SQ IV) has a lower value (0.134 per cent). In previous sections, it was shown that, at this young age, trees on Mt Burr Sand (SQ V) have a greater foliar P concentration than trees on Nangwarry Sand (SQ III).

Table 2.7

Foliar N and P concentration of SQ IV *P.radiata* at 11 years of age in South Australia

Soil type	Nitrogen per cent				Phosphorus per cent			
	Needle age (years)							
	1	2	3	4	1	2	3	4
Nangwarry Sand	1.55	1.34	1.24	1.18	.134	.107	.114	.115
Mt Burr Sand	1.63	1.58	1.48	1.28	.179	.161	.148	.137
Terra Rossa	1.58	1.32	1.23	1.02	.176	.148	.137	.126
Volcanic soil	1.47	1.35	1.29	1.02	.178	.161	.147	.140
Nangwarry Sand* (SQ VII)	1.45	1.33	1.28	1.13	.107	.088	.086	.084

* SQ VII on Nangwarry Sand of the same age is included here for comparative purposes.

Hence, the pattern in this section is similar. It seems that, as the stand develops, foliar P in the Mt Burr Sand trees will drop, but that on Nangwarry Sand may be maintained.

The SQ VII Nangwarry Sand was included for comparative purposes. It has a foliar P percent of only 0.107, well below that usually accepted as being necessary for good growth.

The gradients of foliar P with age are broadly similar at 11 years. The Nangwarry Sand gradient is somewhat less steep but the concentration in 2-year needles in the SQ IV stand is unusually low in relation to that of the 3- and 4-year needles; therefore a definitive statement on differences in gradients cannot be made.

(ii) Foliar N

There is not a great deal of difference, at this age, in foliar N; even in the SQ VII stand on Nangwarry Sand, foliar N concentration is 1.45 per cent compared with the range of 1.47 - 1.63 per cent on the SQ IV soils. As before, there is little difference between N per cent in Nangwarry Sand and Mt Burr Sand and this does contrast with the difference between them in foliar P.

The foliar N/needle age gradient in the Mt Burr Sand differs from that on the other three SQ IV soils at this age. The foliar N per cent is maintained at relatively high levels

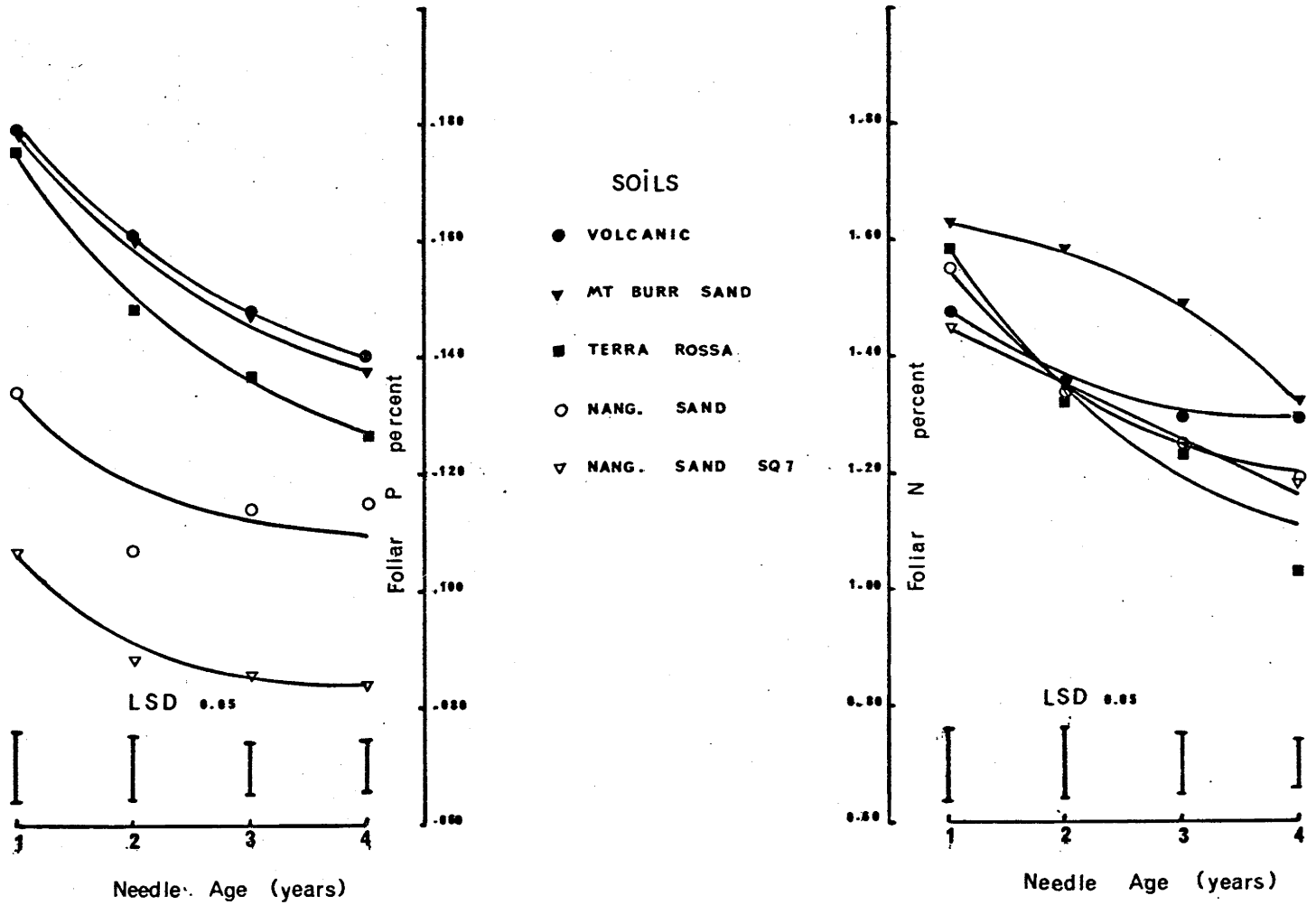

FIG 2.5 Effect of soil type on foliar phosphorus and nitrogen concentration in one to four year needles (see Table 2.7). All stands are site quality IV (with one exception) and 11 years of age.

soils. This Mt Burr Sand pattern differs markedly from that for the 13-year SQ V stand on the same soil (Fig. 2.2). It seems possible that the SQ IV Mt Burr Sand in this section has, in fact, a volcanic or terra-rossa influence or both. All three SQ IV stands sampled (Mt Burr, Terra Rossa and Volcanic) lie adjacent in the one compartment.

2.4 DISCUSSION

In the following discussion, the ways in which age, site quality and soil are related to foliar concentration of nitrogen and phosphorus are reviewed and their possible significance explored.

The pattern of forest growth with time, and hence pattern of nutrient uptake with time, varies with species. Some species have an exceptionally rapid early growth phase reaching a peak very early in the rotation. Other species build up to a peak production over a much longer time period. The main Pinus species planted in Australia have a rapid early growth phase. For example, Pinus radiata stands probably reach maximal basal area increment as early as 6-8 years, and peak volume increment at 10-12 years.

There is a broad pattern of accumulation of mineral nutrients which is closely related to the pattern of dry weight increase; in the case of P. radiata, there is a slow accumulation during the early establishment phase, then a very rapid accumulation over a short period to canopy closure and finally a nearly constant rate of accumulation at less than maximum rates (Forrest 1969). On a moderately good site, for example, the rapid accumulation phase takes place around 5-7 years. An appreciation of nutrient accumulation patterns of the species is necessary to interpret stand age patterns of foliar nutrient concentration.

In the site quality-age series sampled, foliar phosphorus concentration was high at both 10 and 20 years in the SQ V stands on Mt Burr Sand, and relatively low at 30 and 40 years on the same soil. This might be interpreted as follows:

It is possible the Mt Burr Sand growing a SQ V P.radiata forest has a reasonably large pool of available phosphorus when the indigenous eucalypt forest is felled and

converted to pine forest. Where productivity of the site for Pinus is low (e.g., SQ V), then clearly factors other than available phosphorus limit production, so that in the presence of this phosphorus pool, unusually large amounts of phosphorus accumulate in the foliage. However, it is also likely that when this phosphorus pool is exhausted, further phosphorus becomes available from the soil only very slowly. Beyond the stage of peak nutrient accumulation, continuing demand on the soil is reduced, and in fact Forrest (1969) suggests that translocation of phosphorus within the tree to new growth sites may exceed uptake from the soil.

Therefore, in the SQ V stands on Mt Burr Sand, the sharply declining foliar phosphorus levels beyond 20 years suggests a sharply declining rate at which the stand can obtain soil nutrients after that age. By contrast, there is not a pronounced stand age effect on foliar phosphorus for site quality III stands on Nangwarry Sand. At 60 years, a SQ III stand on Nangwarry Sand had as high a foliar-P concentration as a SQ V stand on Mt Burr Sand had at 30 years. What causes this distinctive difference between these two 'Sands'? The elucidation of this could be an important contribution to understanding patterns of productivity through the first rotation and beyond. One factor which may be involved is the moderately high phosphorus-sorbing or fixing capacity of Mt Burr Sand. Raupach (pers.comm.) has shown Mt Burr Sand "fixed" 46 µg out of 200 µg phosphorus added to the soil, but only 1 µg out of 200 µg added to Young Sand was similarly "fixed". Nangwarry Sand, like Young Sand, has very little capacity to sorb phosphorus (Attiwill, pers. comm.). It seems possible that on the lower productive Mt Burr Sand, phosphorus released in the early stages of the Pinus litter decomposition might be largely sorbed by the soil if the amount of phosphorus released by the litter greatly exceeds the amount which can be taken up by the trees. Phosphorus but not nitrogen is in fact rapidly released by raw L-layer litter from an 11-year stand on a Mt Burr Sand (Florence, 1968).

The relationship between foliar phosphorus concentration and stand age is quite different in the SQ II series on Meadow

Podzolic soils, and the contrast might be interpreted in terms of the pattern of phosphorus accumulation on a high quality site. The main production difference between SQ II and SQ V sites is established in the early stages of the rotation when production rates diverge sharply; at a latter stage of the rotation, differences between annual increments are not as large as they are at, say, 10-20 years of age. Correspondingly, accumulation of phosphorus on a SQ II site is probably much more rapid at 10-20 years than it is on SQ V sites. A Meadow Podzolic Sand such as Wandilo Sand has a total phosphorus per cent that is only marginally greater than a Mt Burr Sand. Consequently the amount of phosphorus available for uptake is probably limited, so that during the rapid uptake phase the phosphorus concentration in the large amount of stand foliage produced is diluted, but still within the concentration range associated with good growth. Once the rapid accumulation phase is complete, phosphorus may continue to become available from the soil, and the concentration in the foliage may begin to increase. The SQ III stand on Nangwarry Sand can be regarded as fitting in between the two extremes (SQ V on Mt Burr Sand and SQ II on the Meadow Podzolic); it has not the high foliar-P concentration of the Mt Burr Sand at the earlier ages, but neither does the percentage phosphorus increase with age as it does on the Meadow Podzolic soil.

The needle age/foliar phosphorus gradient has been shown to be characteristic of specific soil groups, and these possibly indicate a stress or potential stress condition not apparent when the foliar content of current year needles only is examined. However, before these gradients can be adequately interpreted, it is necessary to establish how various site factors affect the seasonal pattern of nutrient retranslocation within the tree. Such studies have been made and are described in Chapters 5 and 6.

At this stage, it seems that P.radiata growing on sand might be able to mobilise phosphorus in current needles, thereby maintaining a high level of production, and creating a steep needle age/foliar concentration gradient. The ability to mobilise phosphorus in current needles may indeed be on factor associated

with the productivity of P.radiata forest on sites that are phosphorus deficient for most other crops. As a consequence of the variation in needle age/foliar concentration patterns, the litter layers of stands growing on Sands have lower phosphorus contents than stands having similar wood production and similar current needle foliar phosphorus, but growing on other soils (Florence, 1968). This could have an important bearing on dynamic ecosystem processes at later stages in the rotation.

Unlike phosphorus, needle age/foliar nitrogen gradients tend to be similar for all stands or, at least, differences between site quality classes and soils are not as distinctive as they are for phosphorus.

Nitrogen concentration in current year needles is generally lower on Sands than on Terra Rossa and Transitionals, and lower on the SQ V Mt Burr Sand than the SQ III Nangwarry Sand.

Nitrogen concentration in foliage may remain more stable than phosphorus concentration. For example, in the site quality V stands on Mt Burr Sand, foliar phosphorus per cent was very large at 13 and 21 years and then declined sharply at 30 and 42 years; by contrast foliar nitrogen was constant through ages of 13, 21 and 30 years (around 1.40 per cent) and declined to 1.30 at 42 years. Either nitrogen supply in the soil has not fluctuated as widely as the phosphorus supply, or nitrogen uptake is more controlled than phosphorus uptake, i.e., luxury uptake is less likely with nitrogen than with phosphorus. The foliar nitrogen concentration in the age series on Mt Burr Sand suggests that nitrogen is not particularly limiting by age 40; despite the drop to 1.30 per cent at age 40, the foliar nitrogen/needle age gradient is not steep, and the drop to 1.30 per cent may reflect a general weakening of the trees through phosphorus stress thus affecting uptake of nitrogen. Another example of relative stability in N concentration when P concentration is varying with age is seen in the SQ II stands on Meadow Podzolics and on Mt Muir Sand. Foliar phosphorus rose with age (23, 32, 39 years) but nitrogen concentration in the current needles of the same stands was similar to that of stands at 11, 32 and 39 years.

In summary, the nutrient level/needle age gradients, rather than the nutrient levels in one-year needles, are more strongly related to soil type than to site quality *per se* or stand age. This finding is similar to that of Wehrman (1959) who showed the importance of stratification by soil types in studies of foliar nutrients in European conifer stands.

The present study is not directly related to finding critical or threshold levels of foliar nitrogen and phosphorus. For example, Raupach *et al.* (1969) developed a relationship for diagnostic purposes from data on foliar concentrations in current growth needles, collected on 15 soil types and from a wide range of site classes within the south east of South Australia. As shown by multivariate analysis, about 50% of the variance of the height performance index was accounted for by the foliar N and P contents. This enabled critical and threshold foliar levels to be established. In other words, Raupach *et al.* showed that foliar N and P were related to *current* growth and calculations of the index value based on foliar N and P could be used to determine whether N or P or both were likely to become limiting. The relationship might indicate whether growth in a stand of given site index can be maintained at the rate characteristic of that site index, or alternatively begins to slow down.

The present study has shown that the nutrient level/needle age gradient, and particularly that for phosphorus, is related to the soil mosaic and might be used as an index of a potentially limiting nutrient status. In fact, Heinsdorf (1967) stresses the importance of sampling the whole needle age range to detect potential nutrient stress; and Hausser and Wittich (1969) show that the foliar needle gradient in 1 to 6 year needles was suitable for assessing potential nutrient response, particularly if deviations from a *normal* gradient were considered.

The fact that the nutrient level/needle age gradients, and not the nutrient levels in 1-year needles, are related to soil type does not contradict the results of Raupach *et al.* (loc. cit. that these levels in current growth needles are related to current growth. In fact, if taken together they present a

complete picture. While the nutrient supply regime may be reflected in the nutrient gradient in the whole needle age range, the nutrient levels in the current growth needles are related to current growth.

2.5 CONCLUSIONS

It was found in P.radiata plantations in south east South Australia that :

(1) the nutrient level/needle age gradient in 1-year to 4-year needles was a better index of the nutritional status of the tree than the nutrient levels of N and P in 1-year or current year needles;

(2) the gradient was rather more related to soil type than to site quality at the time of sampling over the whole range of stand age studied i.e., from about 10 to 60 years of age; and

(3) the gradient could be used as an indication of oncoming nutrient status i.e., to detect a potential nutrient stress. The steeper the gradient the more likely would be the future stress.

CHAPTER 3

THE EFFECTS OF SITE ON TREE AND STAND DEVELOPMENT AND FOLIAR NITROGEN AND PHOSPHORUS

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3.1 INTRODUCTION

In Chapter 2 it was shown how foliar nutrient patterns in trees are related to and vary with site factors, particularly soil type, irrespective of the amount of wood volume produced. For a given wood volume production, there may be different nutrient concentrations of foliar N and P at a standard sampling point, and different patterns of N and P in the foliage throughout the crown. Wood volume, however, is only one parameter of stand growth. In this chapter, the exploration of growth/environment/foliar nutrient relations is continued, with particular emphasis on the qualitative aspects of growth, i.e., the distribution of total biomass amongst various tree components, the relationships between the tree components themselves, and the effects of site on foliar N and P patterns.

While most parameters influencing tree quality such as log straightness and shape, branch characters and knot pattern, and wood properties and defect are under genetic control (e.g., Fielding, 1960; 1967c), site plays a major role in phenotypic expression of tree growth and tree characteristics. The extent to which site can influence tree quality may vary between parameters of quality (Johnsson, 1960).

Tree quality in Pinus radiata plantations seems to be particularly affected by site factors; at one extreme trees may have heavy acute-angled branches, rough boles prone to forking, crooked boles and pronounced taper; at the other extreme stands may be uniformly light crowned with almost right-angled branches and single, straight, cylindrical boles. The association of a particular soil type with a particular development of the crown and trunk (for example, coarse branching on certain heavier textured and fertile soils) may be related to the influence of environment (i.e., nutrient supply, moisture regime, etc.), on the growth and development of P.radiata. Fielding (1960) has described, for example, the differences in the development of stands of P.radiata growing on different soil types in the south-east of South Australia: the stands had made approximately the same height growth, but differed markedly in branching and cone production. Most studies on tree quality in P.radiata have

been concerned with stem form, branching and cone production, but only in so far as they affect stem quality (Jacobs, 1938; Fielding 1953; Jacobs, 1954; Fielding, 1960; Fielding and Brown, 1961; Beekhuis and Will, 1965; Fielding, 1967b; Wright, 1968; Wright et al , 1967)

As far as is known, there have been no comparative studies of the way site differences affect tree form and habit (branching and cone production), expressed in terms of the relative dry matter production of bole, foliage and branches. Nor have there been any field studies of possible relationships between tree form and tree nutrition in P.radiata. In Chapter 1, a glasshouse pot trial demonstrated that growth and habit of P.radiata seedlings may be altered by varying the nutrient regime. In the present study, an investigation was made of several stands of P.radiata in the one forest exhibiting marked differences in crown development. The stands occur on different soils, and the differences in crown structure seem to be related to the differences in soil characteristics.

3.2 MATERIALS AND METHODS

3.2.1 The study sites

The investigation was made within Pierce's Creek and Shannon's Flats plantations of the A.C.T. The forest on the study area at Pierce's Creek can be characterised as fine-crowned with regular branching close to right-angles to the stem. On upper slopes, the stands approach a 'spindle-stand' condition and average tree-straightness is good for P.radiata. By contrast, the forest on the site at Shannon's Flats has an apparently greater amount of foliage, and large branches; on the lower slope, particularly, tree straightness is poor and double leaders and ramicorns are more frequent.

The soils at Pierce's Creek and Shannon's Flats respectively are developed from different parent materials. The Pierce's Creek soil is developed from undifferentiated granite of Silurian to Devonian age, while the Shannon's Flats soil is developed from a sandstone-shale formation of Upper Ordovician metamorphosed sediments (Rock types - Bureau of Mineral

Resources Map S 155-16, 1954). The Shannon's Flats soil is a 'red forest loam' with podzolic features. It is a well structured soil with a gradual rather than a distinctive profile differentiation from loam through clay loam to clay. Shannon's Flats receives a high rainfall for the A.C.T., about 36 in. per annum, and the soil supports a wet-sclerophyll native forest over much of the area. However, on upper slopes, the soils are lithosolic, having a high gravel and shale fragment content over fractured parent rock and soil pockets. In such locations the eucalypt forest productivity is much lower.

At Pierce's Creek, the soil is a yellow podzolic. On upper slopes, a shallow A horizon overlies a sharply differentiated clay and decomposing granite parent material. Rainfall at Pierce's Creek is lower than at Shannon's Flats (i.e., 31 in. per annum), and the soil supports a largely dry-sclerophyll native forest. Other climatological data are given in Appendix I.

Physical and chemical analyses were not made on the particular soils used in the present study. However, in a previous study within the same locality (Chuong, 1967), it was shown that the forest loam on shale is superior to the yellow podzolic on granite in terms of both physical characteristics and chemical fertility, i.e., the shale-derived soil has a lower bulk density, a greater percentage of larger soil pores, and greater total N, P, K, Ca and Mg.

3.2.2 The study plots

At each location (Compartment 178, Pierce's Creek and Compartment 407, Shannon's Flats), two 0.1 acre plots were selected, one on an upper slope and the other on the corresponding lower slope, thus giving a productivity range at each location. The plots were so selected that the productivity of the lower slope plot on the Pierce's Creek granite was approximately equivalent to that of the upper slope plot on the Shannon's Flats shale. Plots were 14-16 years of age when the study was made in winter 1969 (Table 3.1).

All plots were nominally planted at 8 x 8 ft spacing. However, some variation in stocking was unavoidable (Table 3.1).

Table 3.1

Details of the study plots at Pierce's Creek and Shannon's Flats (A.C.T.)

Variables	Plot number 1	2	3	4
Location	Pierce's Creek	Pierce's Creek	Shannon's Flats	Shannon's Flats
Age (years)	16	16	14	14
Soil parent material	granite	granite	shale	shale
Slope position	upper	lower	upper	lower
Slope angle (degrees)	25	25	25	25
Slope aspect	S.E.	S.E.	S.W.	S.W.
Stems per acre	640	720	680	570
Stems per hectare	1581	1779	1680	1408
Predominant height* (ft)	54	61	59	64
Basal area per acre	114	156	173	199
Mean d.b.h.o.b. (in.)	5.56	6.23	6.73	7.84
Variation coefficient	0.249	0.249	0.164	0.202
Volume per acre (cu.ft)	1707	3096	3256	6145
Green crown per cent	76.9	62.8	76.3	56.7
	± 2.2	± 5.2	± 2.6	± 3.4

* Mean of four tallest trees per plot of 0.10 acre.

The upper and lower slope plots on the granite-derived soil contain 640 and 720 stems per acre respectively, while the upper and lower slope plots on the shale-derived soil contain 680 and 570 stems per acre respectively. It is the latter plot stocking which was the most problematical. The native forest was more productive on the lower-slope shale soil, and windrows formed at site clearing were larger resulting in greater spacing irregularities where large unburnt logs were avoided at planting. Moreover, weed competition was probably heavy on this site, and some decrease and irregularity in stocking may be attributed to this factor.

3.2.3 Stand sampling

A stand table based on diameter was constructed for each plot. Each stand table was divided into eight diameter classes, containing an equal number of trees. One tree was randomly selected from each diameter class for sampling - i.e., 8 trees were sampled per plot.

For each tree, the sampling procedure was as follows:

(i) The tree was felled as close as possible to ground level.

(ii) Dead branches at the base of the crown were collected for subsequent weighing.

(iii) Green whorls were numbered and recorded by height from the base of the tree; single branches were included in the next whorl above; a whorl was recorded as such where three branches or more arose from about the same level on the bole; ramicorns were counted as single branches and their presence noted; runt branches were disregarded.

(iv) The diameters of all green branches were measured with a vernier-scale caliper as close as possible to the bole surface.

(v) After complete branch diameter enumeration, ten branches were selected from each tree for further analysis; they were used to develop relationships for each plot between branch sectional area, branch-wood weight and foliage weight.

(vi) Foliage samples for chemical analysis were taken from vigorous branches at 20, 40, 60, 80 and 95 per cent of crown height, starting from the crown base. On each branch, needles were kept separate over the needle age range 1-4 years. These foliage samples were oven-dried and analysed using standard techniques (Appendix I).

(vii) All remaining branches were then cut from the tree.

(viii) Bole volume was obtained using the standard sectional method.

(ix) One-foot discs were cut from each 10 ft section of the bole for estimation of bole weight.

(x) Female cones were collected from each tree for dry weight estimation.

3.3 RESULTS

3.3.1 Stand development

The plot measurements (Table 3.1) show a large productivity difference between plots. The four plots form a series of stands of increasing production despite the variation due to stocking irregularities i.e., 1707, 3096, 3256 and 6145 cu.ft per acre for plots 1 and 2 (granite site) and 3 and 4 (shale site) respectively. Plots 2 and 3 permit comparison of stand characteristics on different soils supporting similar wood volume production.

The diameter distributions of the four plots are presented in Table 3.2 and Fig. 3.1. There is a decreasing frequency of stems in the smaller size classes from Plot 1 to Plot 4. For example, Plot 1 has 14 per cent of stems in the 2-3 in. and 3-4 in. diameter classes, whereas Plot 2 has 4 per cent and Plots 3 and 4 have nil per cent in the same classes. If all three smaller classes (i.e., 2-3, 3-4, 4-5 in.) are taken, the percentages are 33, 16, 8.5 and 3.5 per cent on Plots 1,2, 3 and 4 respectively. Consequently, there is an increasing mean diameter in the order of Plots 1, 2, 3 and 4. Moreover, there is also a decreasing variability in diameters as expressed by mean diameters of the plots and their coefficients of variation (Table 3.1). The coefficients of variation in mean diameter are

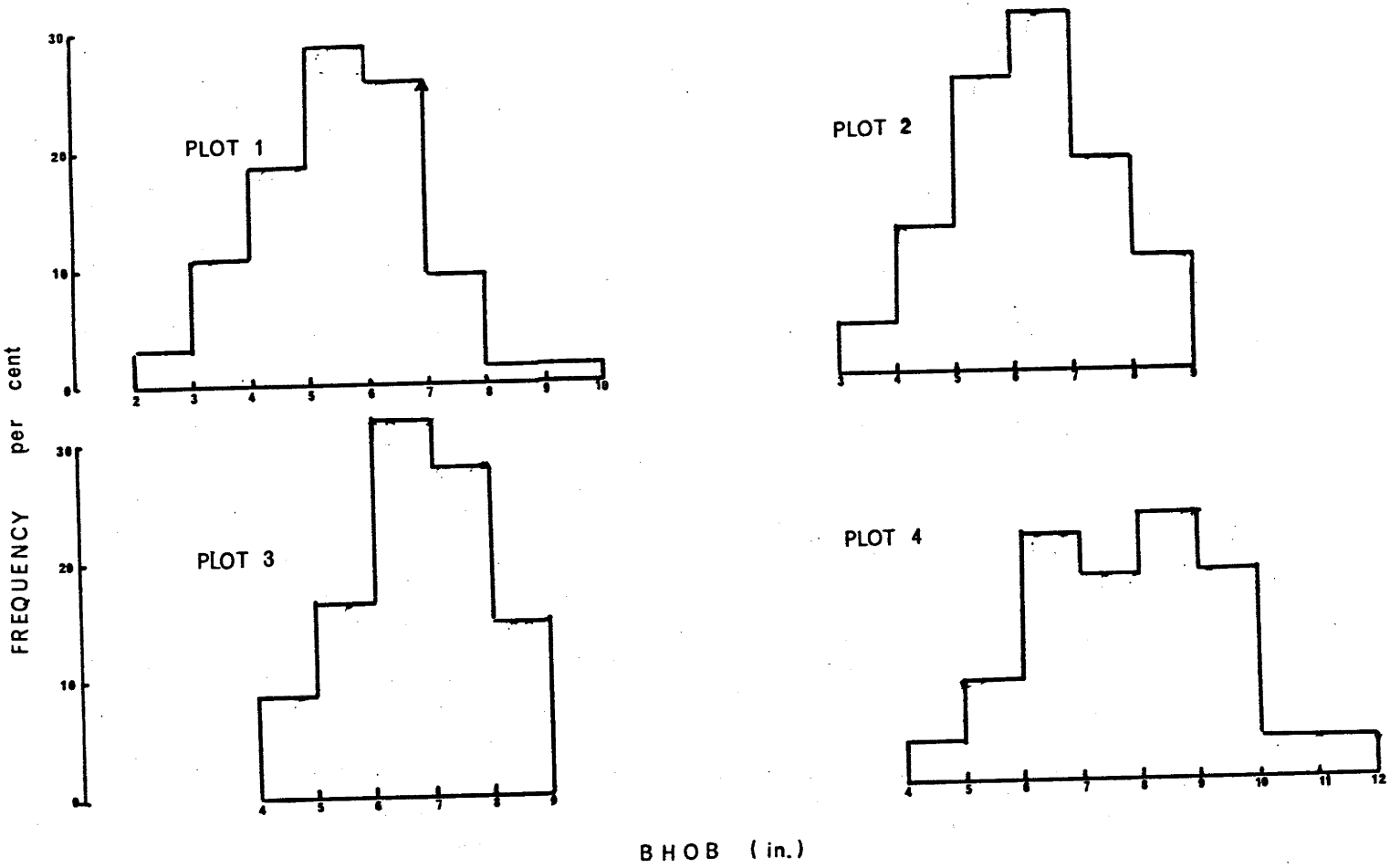

FIG 3.1

Frequency distribution of stems by diameter classes in Plots 1 and 2 (granite-derived soil) and Plots 3 and 4 (shale-derived soil).

0.209 and 0.249 for Plots 1 and 2 on granite, and 0.164 and 0.202 for Plots 3 and 4 on shale. That is, there is a wider diameter range on granite than shale soils. Possibly, this suggests a stronger sorting of crowns into crown classes on the granite derived soil. The per cent green crown in Plot 3 (upper slope on shale) is 76.3 which is significantly greater ($p = 0.01$) than that of Plot 2 (lower slope on granite) viz., 62.8, despite a similar volume production. This again suggests between-tree competition may be greater on the granite than shale soils, leading to a more rapid rise in green crown level. The small difference in stocking between Plots 2 and 3 (i.e., 720 and 680 stems per acre respectively) may account for only a small part of this difference in green crown rise.

3.3.2 Variation in tree taper

Because of the observable differences in crown structure associated with the two soils, differences in tree taper were expected. Two indices of bole form were calculated as follows:

(i) the ratio of total height (ft) to diameter at breast height (4ft 3in.) over bark (in.) (d.b.h.o.b);

(ii) the ratio of total volume underbark (cu.ft) to the product of basal area under bark (b.a.u.b) x height (cu.ft).

Results presented in Table 3.3 indicate there is no significant effect of either soil type or site quality on tree taper, although trees on granite (Plots 1 and 2) tend to have a greater taper, especially on the lower quality site (Plot 1).

Table 3.3

Variation in tree taper between plots on granite-derived soil (Plots 1 and 2) and shale-derived soil (Plots 3 and 4)

Taper expressions	Plot number 1	2	3	4
Ratio of total ht (ft): d.b.h.o.b (in)	7.98	8.76	7.64	7.75*
Ratio of volume (cu.ft): b.a.u.b. x height (cu.ft)	0.531	0.455	0.464	0.464*

* Respective values presented are not significantly different at $P < 0.05$

The extent to which site can influence tree quality may vary between parameters of quality. Johnsson (1960), working with Pinus sylvestris, suggests that stem straightness and taper might be less dependent on the environment than branching, bark, and self-pruning characteristics. Fielding (1967b) showed that P.radiata growing at Jervis Bay (A.C.T.) on infertile sand and at Kowen (A.C.T.) on loam, had different rates of taper as shown by the ratios of diameter at ½ height: height and diameter at breast height: height. However, in an examination of tree taper in four forests of P.radiata differing considerably in soil type and climate in Victoria, Wright (1967) found taper generally varied slightly with site index within any locality; and for stands of similar site index, taper differed between the four localities. Wright suggests the highest taper recorded for the highest quality forest in the four forests examined may be related to the greater branch size recorded for that forest.

In the present study, Plots 2 and 3, growing much in the same climatic locality but on contrasting soils, failed to show any difference in taper. This suggests that environmental differences greater than those examined in this present study may be necessary to induce differences in whole tree taper (e.g., Fielding, 1967b).

An increase in site quality or change to a more fertile soil may be equivalent to an increase in production by, say, fertiliser addition. McKinnell (unpub. data) has shown that P.radiata trees fertilised with N, P, K had increased bole taper due to the production of more wood in the lower bole. In brief, in P.radiata plantations, the influence of soil type on tree taper may be negligible within any climatic locality except in extreme cases (e.g., fertilised stands).

3.3.3 Influence of site on branch production

(a) Number of branches

An analysis of branch production was made in terms of the number of branches per foot of green crown, the number of branches per whorl, and branch production per tree and per acre (Table 3.4).

Table 3.4

Branch and cone production in four plots in the A.C.T.
Plots 1,2 (granite-derived soil)
Plots 3,4 (shale-derived soil)

Variables	Plot number 1	2	3	4
Parent material	Granite		Shale	
Number of branches per tree	105 ±8.5	132 ±18.6	85 ±10.0	85 ±9.1
Number of cones per tree	14 ±3.3	15 ±4.1	5 ±1.4	7 ±2.4
Number of whorls per tree	20 ±1.3	25 ±3.4	16 ±2.3	15 ±1.7
Number of branches per foot of green crown	3.2 ±0.20	3.6 ±0.20	2.2 ±0.20	2.7 ±0.31
Number of whorls per foot of green crown	0.63 ±0.05	0.69 ±0.03	0.41 ±0.05	0.48 ±0.05
Number of branches per whorl	5.3 ±0.29	5.2 ±0.17	5.6 ±0.46	5.6 ±0.21
Number of branches per acre	67000 ±5000	95000 ±13000	57000 ±7000	49000 ±5000
Number of cones per acre	9000 ±2000	10000 ±3000	3300 ±900	3800 ±1400

Soil type has a very marked influence on the number of whorls produced per foot of green crown and the number of branches per foot of green crown. The two plots on the granite-derived soil have a greater mean whorl frequency (0.63 and 0.69 whorls per foot of bole for Plots 1 and 2 respectively) than the two plots on the shale-derived soil (0.41 and 0.48 whorls per foot of bole for Plots 3 and 4 respectively). There is, however, no difference between soil types in the number of branches per whorl. Consequently, plots on the granite-derived soil have a greater number of branches per foot of green crown (3.2 and 3.6 for Plots 1 and 2) than the plots on the shale-derived soil (2.2 and 2.7 branches per foot of green crown for Plots 3 and 4).

Within the one soil type, plot location (lower and upper slope) has no significant influence on the whorl and branch frequency. On both soils, the upper slope plots have a slightly greater number of whorls per foot of green crown than the lower slope plots.

When branch production is presented in terms of total green branches per tree and per acre (Table 3.4), the marked effect of soil type is again evident. The granite-derived soil plots have more branches per tree (105 and 132 for Plots 1 and 2) than the plots on the shale-derived soil (85 for both Plots 3 and 4). They also have more branches per acre (67,000 and 95,000 for Plots 1 and 2 compared with 58,000 and 49,000 for Plots 3 and 4). Despite the large difference in basal area and volume production between Plots 1 and 4, the lower productive Plot 1 has a larger number of branches per acre. On the plots which are fairly comparable in predominant height, basal area and volume production (Plots 2 and 3), the difference in branch production per acre is great, i.e.,95,000 per acre on Plot 2 and 58,000 per acre on Plot 3. Only a small part of the difference between plots on different soils can be attributed to differences in plot stocking and it is clear that the contrasting environments of the granite- and shale-soil sites have strongly influenced branching characteristics. This tends to support the concept of Johnsson (1960) that branching characteristics might be more dependent on the environment than taper and straightness. This,

however, does not deny the strong genetic control of branching characteristics in P.radiata. Cosco (1970) showed that the number of branches per whorl and number of whorls per foot of green crown are strongly inherited in P.radiata.

(b) Size of branches

In the last section it was shown that the edaphic environment had a marked influence on the number of branches produced in stands of P.radiata. The effects of variation in soil type, and of variation in site quality within the one soil type, on branch size are now examined.

In Table 3.5 an analysis is presented for each plot of (i) the total branch sectional area per whorl, (ii) the total branch sectional area per tree and (iii) the total branch sectional area per acre.

While the plots on the granite-derived soil have the greater number of branches, branch size is very much greater on the shale-derived soil. Plots 1 and 2 on the granite soil have branch sectional areas per whorl of 5.7 and 6.9 cm^2 respectively, compared with 13.2 and 13.3 cm^2 for Plots 3 and 4 respectively on the shale-derived soil. There is no difference in branch size between plots on the one soil.

Linear equations relating tree basal area over bark to total branch sectional area for each tree were calculated for each plot (Table 3.5). All equations are highly significant ($P < 0.01$). From these equations, total branch sectional area for the mean tree of each plot and for each plot were calculated (Table 3.5). Because of their larger branches, the shale-derived plots carry a greater branch sectional area per tree and per acre despite their small number of branches per tree and per acre. Plots 3 and 4 have a total branch sectional area of 12.3 and 11.8 m^2 per acre, compared with 7.6 and 9.9 m^2 per acre for plots 1 and 2.

(c) Discussion

Clearly, the environmental difference between the stands has affected branch production. The granite-derived soil has produced a tree with a large number of small branches whereas the shale-derived soil has produced a tree with fewer but much

Table 3.5

Branch sectional area production in four plots in the A.C.T.
Plots 1,2 (granite-derived soil)
Plots 3,4 (shale-derived soil)

Plot No.	cm^2 per whorl	cm^2 per tree	m^2 per acre
1	5.7 ± 0.98	119 ± 14	7.6 ± 0.40
2	6.9 ± 1.51	137 ± 18	9.9 ± 1.28
3	13.2 ± 1.50	190 ± 16	12.9 ± 1.08
4	13.3 ± 2.33	206 ± 24	11.8 ± 1.35

Equations relating branch sectional area (cm^2) to basal area (sq.ft) of individual trees in the four plots of the A.C.T., in the form of:

Total tree branch sectional area (cm^2) =

b x BA (sq.ft) + a

Plot No.	b	a	Correlation coefficient (r)
1	821.8	-19.9	.969**
2	968.5	-67.8	.952**
3	940.8	-42.4	.917**
4	884.6	-90.2	.854**

** indicates significance at $P < 0.01$

larger branches. The smaller difference in environment between plots on the respective soils (i.e.,slope effect) has had little or no influence on the number and size of branches produced.

In this investigation, no significant difference was found in the number of branches per whorl. Wright (1967) also found no significant difference in the number of branches per whorl over a range of sites examined in each of several localities in Victoria. However, the one locality with greatest production had a significantly greater number of branches per whorl than the other three localities ($P < 0.05$). Again, Fielding (1960) found no difference in the number of branches per whorl over a range of sites. Apparently this tree parameter is strongly controlled genetically (Cosco, loc. cit.) and a more extreme environment is needed to vary the parameter.

In the present investigation, although there was little difference in branch size between plots on the one soil, branch size was strikingly influenced by the major environmental difference between the two sites. In his study of P.radiata branching, Wright (1968) found average diameter of branches increased with site index at three out of four localities examined, while at the fourth locality there was no significant increase in branch diameter with increasing site index. Fielding (1967b) observed a similar trend in several small trials in the A.C.T. In the present investigation, while there is a slight increase in branch size with site index on the granite-derived soil, branch size is much more strongly affected by variation in environmental factors not necessarily related to site index itself. This has also been found in studies on New Zealand trees (Bannister, 1962).

3.3.4 Influence of site on branch size and branch weight relationships

On each plot, a total of 80 branches was sampled from the 8 sample trees, and relationships between branch sectional area and branch wood and foliage weight were calculated as simple linear regressions (Table 3.6). All equations are highly significant ($P < 0.001$).

Table 3.6

Regression equations relating individual branch sectional area (S.A. - cm^2) to its foliage (F) and wood weight (W); and branch wood weight to branch foliage weight in the form of :

For W (gm) = b (S.A.) + a

and

W (gm) = b (F) + a

Plot No.	b and S_b +	a	Correlation coefficient (r)
1	F = 26.04 ±1.39 x (S.A.)	- 3.4	0.898***
	W = 61.21 ±2.52 x (S.A.)	- 29.5	0.928***
	W = 2.04 ±0.30 x (F)	- 9.7	0.882***
2	F = 28.62 ±3.77 x (S.A.)	+ 0.5	0.850***
	W = 67.67 ±2.03 x (S.A.)	- 38.2	0.957***
	W = 1.54 ±0.14 x (F)	+ 5.3	0.922***
3	F = 32.68 ±3.32 x (S.A.)	+ 4.5	0.736***
	W = 74.67 ±3.81 x (S.A.)	- 55.9	0.914***
	W = 1.66 ±0.17 x (F)	- 1.1	0.922***
4	F = 27.09 ±2.45 x (S.A.)	+ 7.5	0.777***
	W = 86.55 ±3.75 x (S.A.)	- 92.7	0.934***
	W = 2.22 ±0.28 x (F)	- 24.3	0.916***

S_b + = standard error of regression coefficient b

*** indicates significance at $P < 0.001$

For a branch of a given sectional area, neither site quality nor soil type influences the weight of foliage carried by that branch. The regression lines are not significantly different either in the slope of the line or in the level, i.e., the weight of foliage for a given branch sectional area is constant.

By contrast, for a branch of given sectional area, both site quality variation on the one soil, and the soil variation itself, a significant influence on branch wood weight have ($P < 0.05$).

For a branch of given sectional area then, site quality and soil type do not affect foliage weight but affect branch wood weight. It was thought, therefore, that the relationship between branch wood weight and foliage weight might differ on the four plots (Table 3.6); however, tests of the difference between regression coefficients are not significant. There appears to be no clear influence of site quality and soil type on the branch wood/branch foliage relationship in the four stands examined in the present study.

3.3.5 Influence of site on the relationship between stem size, branch and bole weight and tree volume

In the foregoing sections, the crown structure and the way it is influenced by variation in site quality and environment have been analysed. In this section, an examination is made of the relationship between tree size, tree volume and the weight of various components of the tree.

A series of linear regressions was calculated relating the following:

(a) Basal area over bark (B.A.O.B) and foliage weight
(b) B.A.O.B. and branch weight
(c) B.A.O.B. and weight of bole wood
(d) B.A.O.B. and tree volume

The linear regressions are given in Table 3.7 together with the regression coefficients, their levels of significance and standard errors. The various relationships are presented graphically in Figs. 3.2-3.3.

Table 3.7

Relationships between tree basal area (B.A. - sq.ft) and volume u.b. (cu.ft) and tree component weights (kg) respectively in the form of:

$$y = b\ (B.A.) + a$$

(Sb = standard error of b, and r = correlation coefficient)

Variables & plot no.	b	S_b	a	r
Vol. u.b.				
Plot 1	15.49	±1.81	+ 0.06	0.844xx
2	24.62	±1.90	- 0.91	0.989xx
3	22.84	±1.88	- 0.85	0.869xx
4	26.24	±1.82	- 1.37	0.841xx
Foliage Wt				
Plot 1	20.03	±1.09	- 0.39	0.829x
2	26.87	±4.28	- 2.03	0.793x
3	22.14	±3.88	- 0.92	0.799x
4	25.12	±3.40	- 2.73	0.830x
Branchwood Wt				
Plot 1	53.79	± 8.18	- 1.43	0.721x
2	69.71	±11.07	- 5.71	0.793x
3	92.02	±14.78	- 5.16	0.794x
4	81.60	±10.96	-10.37	0.830x
Bole Wt				
Plot 1	255.3	±41.6	- 1.43	0.818x
2	337.3	±27.9	- 2.06	0.989xx
3	317.6	±30.1	- 3.62	0.971xx
4	406.5	±24.5	-29.71	0.989xx

x indicates significance at $P < 0.05$

xx indicates significance at $P < 0.01$

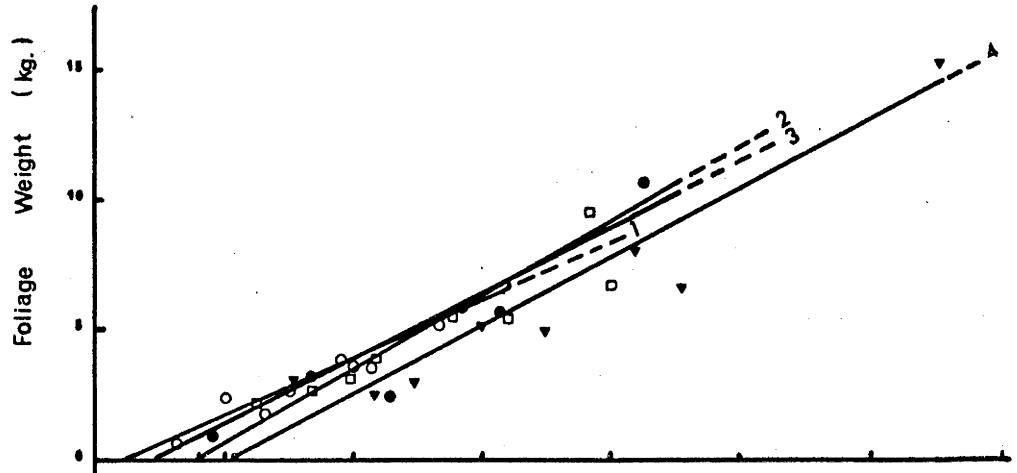

FIG 3.2

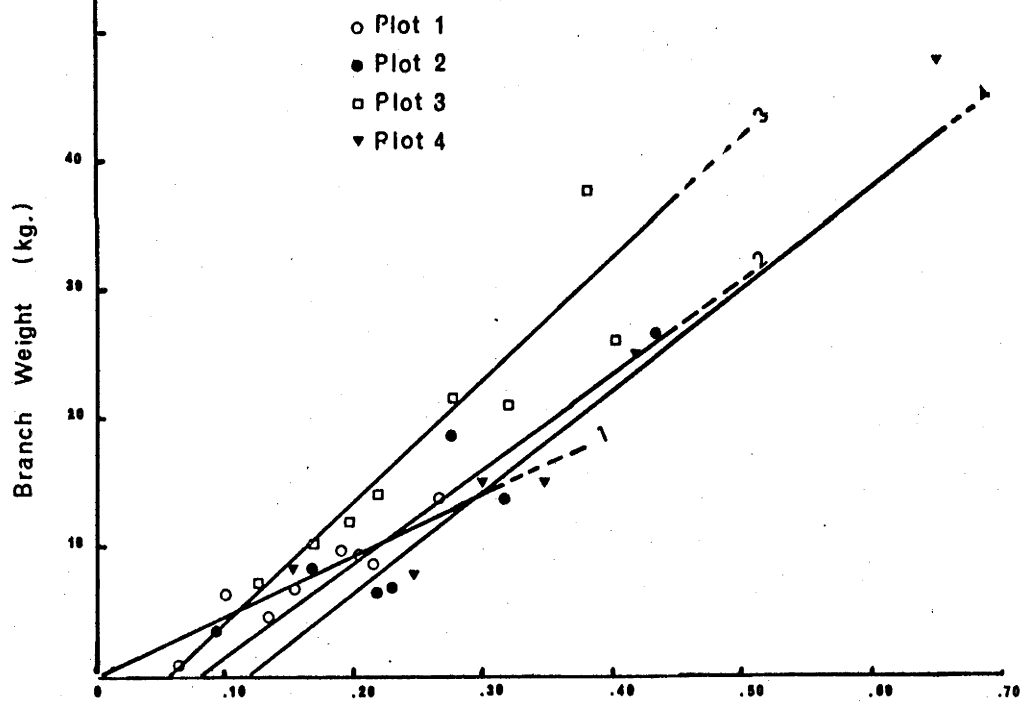

FIG 3.3

Relationship between individual tree basal area and foliage weight (Fig. 3.2) and branch weight (Fig. 3.3) respectively, for Plots 1 and 2 (granite-derived soil) and Plots 3 and 4 (shale-derived soil). (See Table 3.7).

(a) Relationship between B.A.O.B. and foliage weight

For a tree of a given basal area, there is no significant difference between the four stands in foliage weight. Differences in the regression constants are not significant.

(b) B.A.O.B. and weights of branch wood

Here again, for a tree of given basal area, there is no significant difference between the four stands in branch wood weight, except perhaps in stand 3 which just missed significance at $P < 0.05$. This will be reflected, however, in total branch weight per plot (Section 3.3.6).

(c) B.A.O.B. and weight of bole wood

Only Plot 4 has a significantly higher slope than Plot 1 ($P < 0.01$). This means that, except in the "extreme" stands (Plots 1 and 4), a tree of a given basal area has a similar bole weight irrespective of soil and site quality.

(d) B.A.O.B. and tree volume

For a tree of a given basal area, the volume underbark is similar for three stands (Plots 2, 3 and 4) and all three have a significantly greater slope than Plot 1 ($P < 0.01$). This means that for a tree of a given basal area, volume is less in Plot 1 than in the other three plots, particularly at upper levels of the tree B.A. range.

(e) Discussion

Despite the large difference in crown structure and volume production in the four stands, relationships between individual tree B.A. and tree foliage weight, branch weight and bole weight respectively, are remarkably uniform. The only differences between plots, in the several relationships examined, are those between the "extreme" Plots 1 and 4, where the relationships between basal area and volume and basal area and bole wood differ ; and that involving Plots 1 and 3 in the relationship between basal area and branch wood. In Pinus radiata then, there is a strong tendency for a tree of a given size to have similar weight in its component parts despite large differences in site and in crown structure.

3.3.6 Total production and distribution of biomass

Using a series of regression relationships derived between tree basal area and the weight of various tree components (Table 3.7) and the plot stand tables (Section 3.2.3) production of foliage and branch and bole wood per hectare has been calculated (Table 3.8). Percentage distribution of biomass amongst these three components is given in Table 3.9.

Within each soil, the percentage of biomass in bole wood is greater on lower slope plots ($P < 0.05$). On Plot 4, the per cent biomass is 82.5 and this is significantly greater than the 77.2 per cent for Plot 3 and 79.6 per cent for Plot 1; Plot 2 has greater between-tree variability and the 83.8 per cent bole wood just falls short of significance. For plots on different soils similarly located with respect to slope position, per cent bole wood does not differ.

Because the upper slope plots have a lower percentage of bole wood, they have a greater percentage production of branches and foliage. The upper slope plot on shale (Plot 3) has a greater percentage of total production in branch wood (18.1) than the other three plots (12.1 - 14.6); and the upper slope plot on granite (Plot 1) has a greater percentage of biomass in foliage (5.7) than the other three plots (4.0 - 4.7).

To compare the relative biomass distribution in the four plots further, ratios of foliage weight to (1) bole weight, (2) branch weight, and (3) bole plus branch weight, have been calculated (Table 3.10). The weight of bole plus branch weight per unit of leaf weight is closely similar for the three more productive stands (20.3 to 21.9), but the ratio is lower for the low-quality Plot 1 (16.5).

In summary, variation in soil type may have little effect on the distribution of biomass in P.radiata stands or on the weight of foliage on a branch of given sectional area, but its effects on characteristics of branch production (number and size) may be great. Possibly due to an insufficiency of data in the present study, the site quality (slope) effect is unclear, except that a poor site (approaching

Table 3.8

Dry matter production per ha. for *P.radiata* in the A.C.T.

(Plots 1 and 2 on granite derived soil; Plots 3 and 4 on shale derived soil) (Unit = 1000 kg)

Plot	S.Q.	Age (yrs)	Foliage ± S.E.	Branch ± S.E.	Bole ± S.E.	Total ± S.E.
1	V^-	16	4.74 ± 0.45	12.08 ± 0.80	65.80 ± 4.10	82.63 ± 5.34
2	IV*	16	6.52 ± 0.90	19.64 ± 2.33	123.35 ± 5.57	149.52 ± 8.80
3	IV	14	7.64 ± 0.62	29.53 ± 2.35	125.77 ± 5.17	162.94 ± 8.15
4	II**	14	8.01 ± 0.72	23.94 ± 0.73	150.09 ± 5.20	182.04 ± 6.65

* approaching IV^- (Jacobs, 1962)

** approaching II^+ (Jacobs, 1962)

Relative proportion of biomass in foliage, branches and bole in four stands of P.radiata varying in site quality (S.Q.) and growing on different soils

Table 3.9

Component weight as a percentage of total weight (F+Br+Bole) where F = foliage, Br = branch, and Bole = bole weight

Plot No.	S.Q.[x]	Foliage	Branches	Bole
1	V-	5.74	14.62	79.6
2	IV	4.01	12.08	83.8
3	IV	4.69	18.12	77.2
4	II	4.40	13.15	82.5

x = based on data of Jacobs (1962)

| Values connected by a line are not significantly different at $P < 0.05$.

Table 3.10

Ratios of foliage weight : branch weight, and foliage weight : bole weight

F = foliage, Br = branch

Plot No.	S.Q.	F : Br	F : Bole	F : Total Weight
1	V-	1 : 2.6	1 : 13.9	1 : 16.5
2	IV	1 : 3.0	1 : 18.9	1 : 21.9
3	IV	1 : 3.9	1 : 16.5	1 : 20.4
4	II	1 : 3.0	1 : 18.8	1 : 21.8

"spindle stand" condition) may be less efficient in wood production per unit of leaf weight.

3.3.7 Foliar nitrogen and phosphorus patterns

A study of foliar nutrient concentration and pattern within tree crowns was made on each of the four study plots. Within each plot, foliage samples were collected from the eight sample trees (Section 3.2.1). These were taken from vigorous branches at 20, 40, 60, 80 and 95 per cent of crown height, starting from the crown base. On each branch, needles were kept separate over the needle-age range 1 - 4 years. An examination was made of nitrogen and phosphorus concentrations, and the way they vary with respect to soil type, slope position within a soil type, position in crown, and needle age.

(a) Influence of soil type and slope position

On the granite-derived soil, mean foliar N content of 1-year needles on the 1-year whorl was the same for both plots (upper slope and lower slope) viz., 1.56 per cent (Table 3.11). On the shale-derived soil, foliar N concentration was greater, but again similar for both plots - 1.83 and 1.80 per cent respectively. The difference between the foliar N levels associated with the two soils is significant ($P < 0.02$).

By contrast, foliar P per cent increases with site quality on both soils; the difference between the upper-slope granite plot (0.180 per cent) and the lower slope plot (0.260 per cent) is significant ($P < 0.02$) but that between the upper and lower slope plots on shale is not significant (0.216 and 0.268 per cent, respectively), although the trend is similar to that on the granite (Table 3.11).

Trees growing on shale-derived soil, therefore, have a greater foliar N per cent irrespective of plot location. The reverse applies to foliar P which is affected more by plot location (and site quality) than by soil.

(b) Effect of crown position

Within each plot, an analysis was made of variation in foliar N and P in 1-year needles at the five crown positions

Table 3.11

Variation in foliar N and P per cent with crown position in P.radiata (14-16 yrs) in the A.C.T. (Winter sampling)

(Plots 1 and 2 on granite-derived soil; Plots 3 and 4 on shale-derived soil)

Crown position	Plot No.	N	P
95% crown ht. (current needles)	1	* 1.56	0.180
	2	1.56	* 0.260
	3	1.83	0.216
	4	1.83	0.268

		Needle age (yrs)							
		1	2	3	4	1	2	3	4
Mean of 5 posit.**	1	1.60	1.45	1.26	1.04	0.171	0.145	0.133	0.118
Mean of 5 posit.**	2	1.53	1.49	1.27	1.12	0.207	0.188	0.173	0.146
Crown ht : 95%	3&4***	1.82				0.200	0.165	0.150	0.140
80%		1.77	1.67	1.40					
60%		1.66	1.52	1.24	1.14				
40%		1.60	1.46	1.24	1.06				
20%		1.52	1.33	1.18	1.02				

* values connected by a line are not significantly different at $P < 0.05$

** 5 positions in the crown, namely, 20, 40, 60, 80 and 95 per cent of crown height. F-test shows no significant difference between 5 levels ($P < 0.05$).

*** Plots 3 and 4 are combined because there is no difference between plots. There is a significant difference between crown levels in N but not in P.

sampled, i.e.,at 20, 40, 60, 80 and 95 per cent of crown height. When concentrations of N and P are compared at different crown positions (Table 3.11), the F ratios and the significance of the F ratios are as follows:

Plot	F-ratios for N per cent		F-ratios for P per cent		N : P ratio
1	F(4/35 d.f.)= 1.46	NS*	1.06	NS	8.7
2	= 1.18	NS*	2.26	NS	6.0
3	= 3.20	P<0.05	2.09	NS	8.5
4	= 3.46	P<0.05	1.43	NS	6.7

* F for 4/35 d.f. for P < 0.05 is 2.65

Foliar P does not vary with crown position on any plot.

Foliar N does not vary with crown position on the granite-derived soil plots but does so on the shale-derived soil plots.

It is surprising that foliar phosphorus does not vary significantly with crown position on any plot, particularly on the more vigorous plots 3 and 4. Foliar phosphorus levels on all plots are relatively large, even on Plot 1 (0.180 per cent). The large uptake of phosphorus could account for the lack of a vertical gradient, but this question could only be resolved by a study of the way tree vigour and phosphorus supply influence phosphorus gradients in crowns of P.radiata.

There is a vertical gradient in foliar N concentration only on the shale-derived soils where it ranges from 1.8 (at 95 per cent crown level) to 1.5 per cent (20 per cent crown level). The vertical N gradient occurs on the plots with the greater levels in foliar N i.e., 1.83 per cent in current needles in the upper crown Plots 3 and 4, compared with 1.56 per cent in those of Plots 1 and 2. Again, any interpretation of this difference in foliar N gradient must await detailed examination of the effects of tree vigour and N supply on the gradient (Chapter 5).

(d) Effect of needle age on foliar N and P levels

Foliar N and P levels in needles of varying age are given in Table 3.11 and the needle age/foliar nutrient relationships are illustrated in Fig. 3.4. There is little or no difference between plots in the nature of the N and P gradients. The foliar P gradients are close to linear and differ in this respect from gradients shown for P.radiata on sand soils in South Australia (Chapter 2). Rather they are more like the needle age/foliar P gradients associated with the terra rossa and terra rossa-sand transitionals. This absence of a steeper gradient may be related to the rather greater phosphorus concentration on these plots than on the sand dune soils in South Australia. The data suggest little phosphorus stress on any of the plots. The foliar N/needle age gradients are again similar to those recorded for good quality stands in other studies; the gradient is slightly steeper in Plots 3 and 4. Despite the greater foliar N concentration of the shale-soil plots, the foliar N/needle age gradient is somewhat greater than that of plots on granite soil. This pattern is similar to the vertical N-concentration gradient found in 1-year needles in the four plots.

3.4 CONCLUSION

The most striking feature of the present study is the effect of environmental variation (soil type) on crown structure i.e., the number and size of branches. By contrast, the same environmental variation had little effect on tree taper, distribution of biomass between various tree components, or on weight of bole wood per unit of foliage weight. Despite large differences in crown structure, a tree of the same basal area on all four plots had similar volume and similar branch, foliage and bole wood weight.

Without a detailed experimental analysis of the ecosystem it is impossible to determine what environmental factors are primarily responsible for the differences in crown structure. With respect to the patterns of foliar N and P, the shale-soil stands differed from the granite-soil stands in having, at

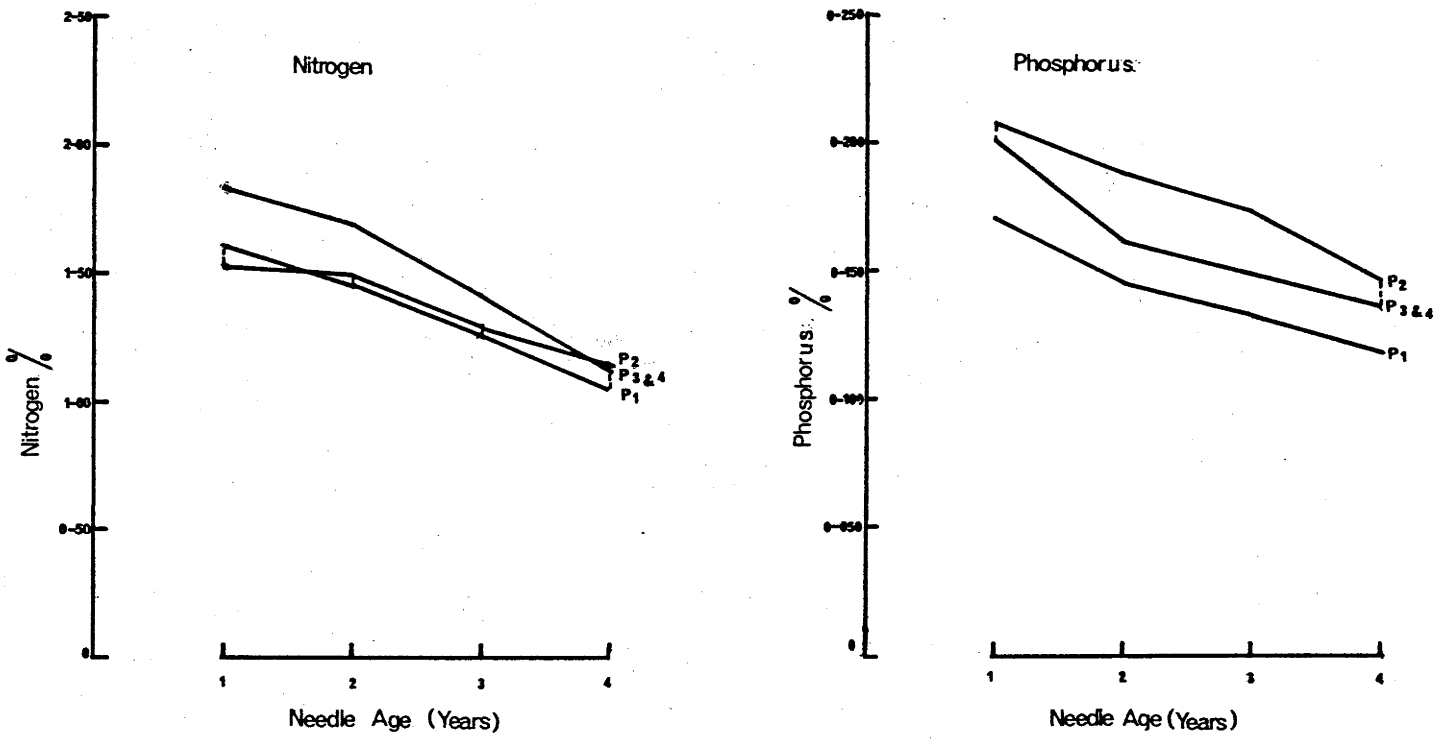

FIG 3.4

Foliar nutrient/needle age gradients for trees in Plots 1 and 2 (granite-derived soil) and Plots 3 and 4 (shale-derived soil). (See Table 3.11).

comparable positions on the slope, better stand vigour; a higher concentration of foliar N and a vertical gradient in this nutrient. Phosphorus concentration was less affected by soil type than position on the slope and there was no significant vertical gradient of the nutrient on either soil.

Whether or not differences between stands in foliar nitrogen concentration and pattern influence crown structure needs further study. It will be necessary, in the first instance, to determine what interpretation might be placed on the existence of a vertical foliar N gradient in one stand and not in another, and this is attempted in Chapter 5; it will then be necessary to examine many situations where growth varies qualitatively in a similar way to that of the present study, to determine what measurable tree and environmental parameters are consistently related to such variation; and finally, experimental evidence will be needed to show how manipulation of specific environmental factors affects tree and crown characteristics.

3.5 SUMMARY

An investigation was made of four 14-16 year old stands of Pinus radiata in the one locality in the A.C.T. The stands occur on different soils and have marked differences in crown structure which seem to be related to differences in soil characteristics.

The most striking feature of the study is the effect of environmental variation (soil type) on crown structure i.e. the number and size of branches. The shale-soil stands had fewer but larger branches than the granite-soil stands. By contrast, the same environmental variation had little effect on whole tree taper, distribution of biomass between various tree components, or on weight of bole wood per unit of foliage weight. Despite large differences in crown structure, a tree of the same basal area on all four plots had similar volume and similar weight of branches, foliage and bole wood.

Foliar nitrogen and phosphorus concentration and patterns within the crown were also studied. Differences between plots were detected but whether or not the differences have influenced crown structure needs further study.

CHAPTER 4

ACCUMULATION AND DISTRIBUTION OF FOLIAGE AND FOLIAR NUTRIENTS ON A LOW QUALITY SITE

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4.1 INTRODUCTION

A large part of plantation forestry in Australia is associated with soils that are deficient in nutrients particularly nitrogen and phosphorus. Again, many plantations are established on shallow or stony soils where available moisture is the main factor limiting growth. Yet Pinus radiata is capable of producing, by world standards, large amounts of wood on a wide range of sites, including those deficient in available nutrients, water or both.

In a study carried out within a moderately high quality P.radiata forest at Tumut, N.S.W., Forrest (1969) explored the nature of the demand by P.radiata on the soil nutrient resource. He examined the pattern of dry weight and nutrient accumulation, and the pattern of nutrient distribution in tree crowns over the age range three to twelve years. Peak foliage weight and peak total weight of nutrients contained in crowns occurred at five to seven years, and were associated with canopy closure. Thereafter, foliage weight and nutrient weight remained more or less constant. After crown closure, the phosphorus required for bole and crown production is small with much of the phosphorus accumulated in new canopy growth each year coming from an internal redistribution from older needles. Translocation of phosphorus from this stage onwards may, in fact, exceed uptake from soil. But what of the pattern on sites which are much less productive? Is the period of peak dry matter production and accumulation of nutrients delayed until canopy closure, which occurs at a later age on low quality sites? Do foliage and nutrient weights remain more or less constant after the peak? Is the relative distribution of total dry matter production to foliage, branches and bole any different on low-production sites?

Furthermore, to understand the significance of foliar nitrogen and phosphorus on any one site, it is essential to understand the patterns of accumulation and distribution of nutrients in the tree foliage, and the relative distribution of nutrients in the needles of different ages and at different locations within the tree crown.

Consequently, the present study aims to examine

(1) the pattern of above-ground dry matter accumulation and distribution (excluding litter) in a low quality P.radiata stand;

(2) the accumulation of nitrogen and phosphorus in the foliage as a whole, and their distribution in needles of different ages; and

(3) to interpret in terms of (1) and (2) the nutrient status of the tree as indicated by the three foliar indices as outlined in the introductory chapter, i.e.,

   (a) the N and P concentration in 1-year needles at or near the apex of the tree;

   (b) the vertical gradient of N and P in current year needles from apex to crown base;

   (c) the horizontal gradient of N and P at a specified level in the crown through the age range of needles.

4.2 MATERIALS AND METHODS

4.2.1 Suitability of study plots

An age-sequence of stands of 7½, 11½, 14½ and 17½ years old was selected in Kowen Forest in the A.C.T. Kowen Forest is a P.radiata plantation of about 6,000 acres. Because of low annual rainfall (about 25 in.) and generally shallow soils, the area is marginal for radiata pine. Nevertheless, it is regarded as a useful plantation site because of its close proximity to an expanding market, i.e., Canberra.

Considerable difficulty was experienced in selecting areas within specified ages which were comparable with respect to site index and stocking. Indeed this was impossible because of variation in planting spacing, deaths of trees in drier years and thinning of malformed trees due to drought. A large variation in basal area and volume of stands of the same age and site index is apparently a characteristic of this low quality forest (Carron, 1967).

4.2.2 Structure of study plots

Four plots of similar site index were chosen, using a set of stand top height/age curves for Kowen Forest (Carron,

loc.cit.). One 0.1 acre plot was established at each selected location. Details of climatic factors and soil types are described in Appendix I. Stand tables were prepared and are presented graphically (Fig. 4.1). Despite stocking differences, the plot predominant heights (mean of four tallest trees per 0.1 acre) fit reasonably well Carron's stand top height/age curves for stands of similar site index on this forest (Fig. 4.2). The plots would represent site quality classes VI - VII on South Australian standards (Jacobs, 1962; Lewis, 1963). Their residual stockings are quite different, and for some purposes they might better be thought of as covering two separate age sequences, as follows (also see Table 4.1):

(a) 7½ years (480 trees per acre) - 14½ years (490 trees per acre)

(b) 11½ years (610 trees per acre) - 17½ years (610 trees per acre)

Despite differences in stocking, the plot basal area curve is parallel to one established by Carron (1967) for plots of similar site index (Fig. 4.2); the slope of this curve is similar to that for SQ VI - VII in South Australia in the same age range.

Because the present study is particularly concerned with the broader perspective of total stand dry weight production and foliage nutrient accumulation and distribution, the unavoidable differences in plot stocking were not regarded as a critical barrier to their use. Variation in stocking was expected to affect size of the individual trees, but marked influences of stocking on stand parameters such as branch weight and foliage weight were not expected. The hypothesis of Möller (1947) that leaf weight is independent of site, and both leaf weight and total production are relatively independent of stand density was generally accepted. However, the influence of stocking on these parameters has been found to be pronounced, and in fact the inclusion of two stocking levels in the series has contributed to a deeper understanding of growth and nutrition on low production sites.

Because of the shallow and stony nature of soils at Kowen Forest, pre-planting ripping has been carried out for many

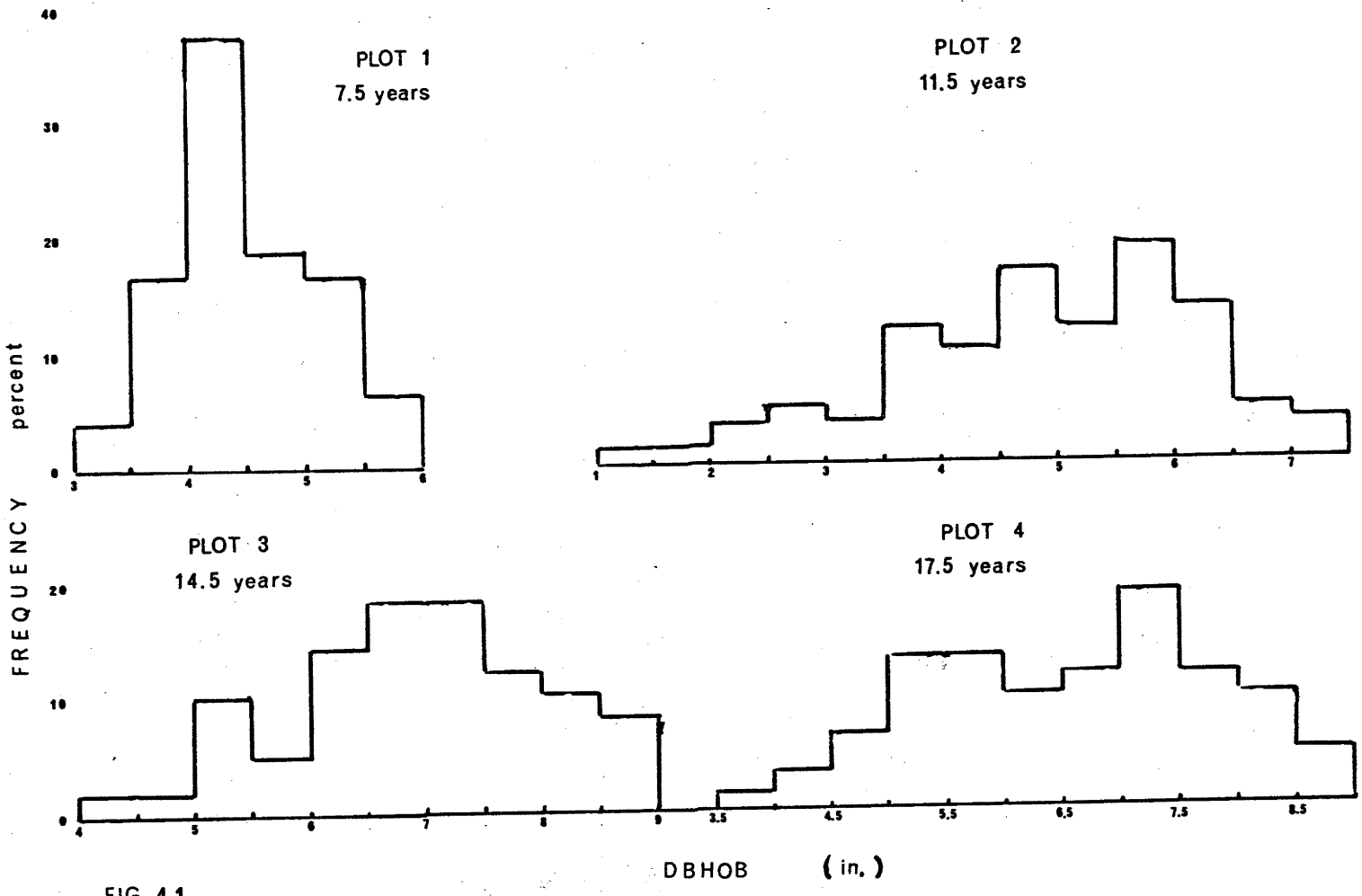

FIG 4.1

Frequency distribution of stems by diameter classes in four stands of an age-sequence in Kowen forest.

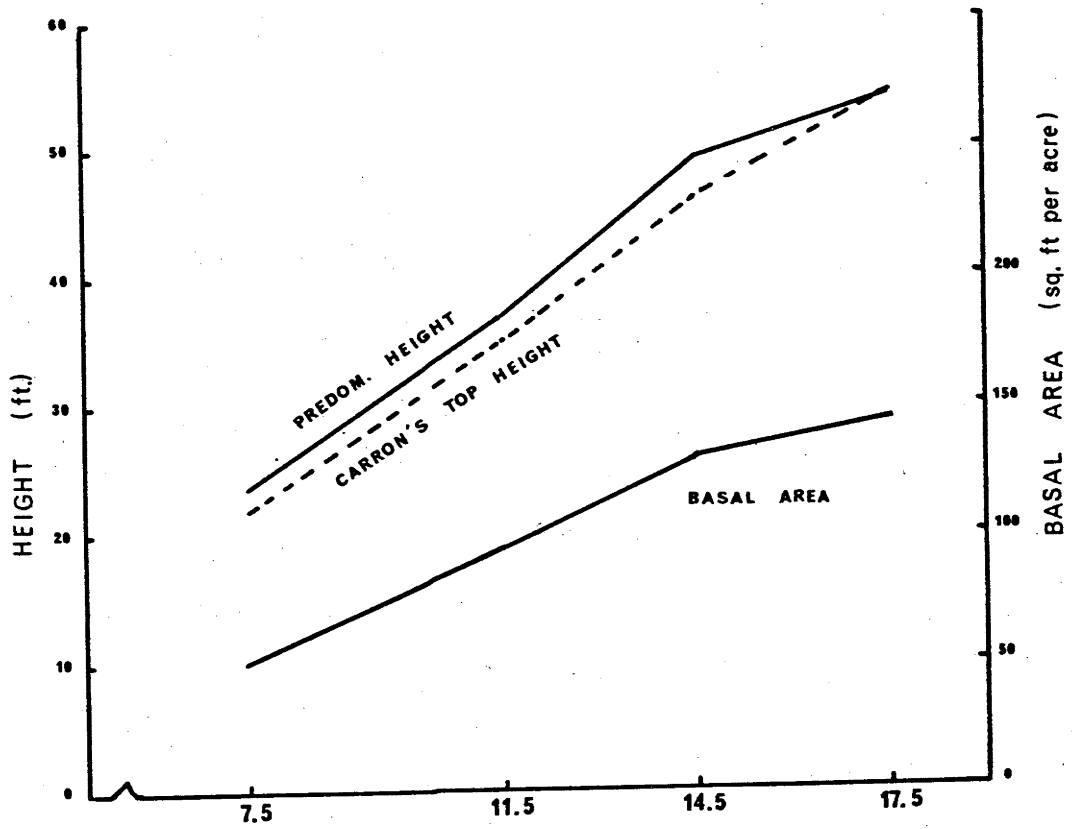

FIG 4.2

Predominant height and basal area curves for an age-sequence plots at Kowen forest. A stand top height/ age curve for stands of similar site index on this forest is also shown (see Carron, 1967).

TABLE 4.1

Details of an age-sequence of stands at Kowen (A.C.T.)

Parameters	Age (February, 1969) 7½	11½	14½	17½
Compartment	123	80	59	53
Predominant ht (ft)+	23.8	36.7	49.0	53.5
Stems/acre	480	610	490	610
Stems/ha.	1186	1507	1211	1507
B.A. (sq.ft/acre)	50.6	94.0	129.4	114.2
Mean tree D.B.H.O.B. (in.)	4.4 ± 0.09	4.8 ± 0.18	6.9 ± 0.16	6.5 ± 0.16
Mean tree B.A. (sq.ft)	0.1046	0.1272	0.2574	0.2276

+ Predominant height = average of 4 tallest trees in plot of 0.10 acres.

years, including the areas sampled in this study. Ground pruning is also a standard practice, but in this age sequence, only the 11½ -year plot was pruned up to eight feet. Branch and foliage weight and hence nutrient weight have been adjusted on this plot to take into account pruning losses using the percentage correction factor (circa 30 per cent) used by Forrest (1969) in a similar investigation on a better quality site.

4.2.3 Sampling

Within each plot, a stratified random sample of eight trees was made, and using these trees, regression equations were derived relating individual tree basal areas to a number of bole and crown parameters. The sampling sequence on each plot was as follows:

(1) Bole diameter at breast height over bark (D.B.H.O.B.) was measured for each tree. This diameter distribution was divided into eight diameter classes, with an equal number of trees in each class. One tree was randomly selected from each diameter class for dry weight assessment and nutrient analysis. Harvesting of all 32 trees on the four plots was carried out in February 1969.

(2) Each tree was felled by cutting at ground level. The bole of the tree was separated into six age strata by identifying distinctive winter nodes along the boles (Jacobs, 1936). The age strata identified were as follows:
   (a) current year section
   (b) 2 year section
   (c) 3 year section
   (d) 4 and 5 year section
   (e) 6 and 7 year section
   (f) section more than 7 years

(3) All branch and foliar material in the 1-year, 2-year and 3-year strata were collected for oven-drying and weighing.

(4) In each of the 4-5 year, 6-7 year and 7+ year strata, all branches were cut and total branch and foliage fresh weight were obtained immediately using field scales sensitive to 4 gm, i.e., total fresh weight of all crown

material at and below the 4-year branch whorl was obtained in the field. Before cutting the branches from the bole, a random sample of branches along the bole section was taken and weighed separately. The sample was approximately equal to 25-30 per cent of total branch and foliage fresh weight. It was taken to the laboratory for oven drying and weighing.

(5) A one-foot disc was cut from each five-foot section of bole.

(6) Within each bole stratum, the material was further divided into needles and branches of varying age, separately dried and weighed.

(7) All female cones on each tree were collected and oven dried.

(8) All dead branches were collected from each tree; these were weighed in the field and a sample taken for drying and weighing to permit conversion of branch weight to a dry-weight basis.

4.3 RESULTS I : DRY WEIGHT PRODUCTION

4.3.1 Distribution of dry weight as a function of stand age

Regression equations were derived for each plot relating basal area to foliage weight, branch weight and bole weight respectively. The details of regression methods for tree biomass estimation are given by Ovington et al. (1967).

The regression equations are of the form:

$$\underset{(kg.)}{\text{Weight}} = b \times \underset{(sq.ft)}{(\text{Basal area over bark})} + a$$

and are summarised in Table 4.2.

All equations are significant except those for branch weight and foliage weight in the 7½-year old stand. This particular stand had unusual variability in branch and foliage weight for trees of similar d.b.h.; for example, compare trees nos. 4, 5 and 6 in Table 4.3. For this 7½-year plot, component weights were calculated for a tree of mean d.b.h.o.b. (4.38 in.) using the regression equations. These are as follows:

Table 4.2

Regression equations relating dry weight of tree components (kg.) and tree basal area (sq.ft) in the form of:

Dry weight = b x B.A. + a

Dry weight (kg.)	Stand age (years)	b	a	r	Significance of r
Foliage weight	7½	36.109	+ 3.649	0.625	N.S.
	11½	23.342	- 0.085	0.806	$p < 0.05$
	14½	35.900	- 4.062	0.750	$p < 0.05$
	17½	19.534	- 1.731	0.818	$p < 0.05$
Branch weight	7½	63.214	+ 3.178	0.579	N.S.
	11½	31.455	- 0.428	0.860	$p < 0.01$
	14½	60.456	- 7.370	0.837	$p < 0.01$
	17½	43.986	- 4.878	0.766	$p < 0.01$
Bole weight	7½	204.84	+ 0.21	0.825	$p < 0.05$
	11½	296.81	- 6.08	0.869	$p < 0.01$
	14½	265.47	-10.23	0.840	$p < 0.01$
	17½	291.61	+ 1.77	0.849	$p < 0.01$
Total above ground including cones but excluding dead branches	7½	351.44	- 5.61	0.872	$p < 0.01$
	11½	365.42	- 5.45	0.889	$p < 0.01$
	14½	368.95	-22.51	0.848	$p < 0.01$
	17½	300.24	- 7.84	0.830	$p < 0.01$

TABLE 4.3

Dry Weights and Nutrient Weights (in the Foliage only)
of Sample Trees in the Age Sequence at Kowen (A.C.T.)

Stand Age (Years)	Variables	Tree No. 1	2	3	4	5	6	7	8
7½	D.B.H.O.B. (in)	3.26	3.76	4.13	4.24	4.30	4.60	5.14	5.48
	Foliage (kg)	3.435	6.907	7.806	8.578	7.013	9.341	8.191	8.375
	Branch (kg)	4.874	7.845	8.590	11.470	7.062	14.842	13.873	10.173
	Bole (plus bark) (kg)	10.859	11.411	21.758	22.853	23.308	22.043	27.874	34.295
	Cones (kg)	-	.203	-	.547	.810	-	.064	-
	Dead branches (kg)	-	-	-	-	-	-	-	-
	Total (excluding dead branches) (kg)	19.168	26.366	38.154	43.148	38.193	46.226	49.975	52.843
	Foliar nitrogen (gm)	21.35	80.42	87.44	100.28	81.79	105.82	90.62	86.28
	Foliar hosphorus (gm)	5.665	8.145	9.726	12.907	9.626	13.054	12.261	11.154
11½	D.B.H.O.B. (in)	2.50	3.76	4.20	4.52	5.10	5.86	6.24	5.64
	Foliage (kg)	1.085	1.689	1.790	3.004	3.112	3.207	4.373	6.754
	Branch (kg)	.586	1.801	2.377	3.221	4.328	5.691	6.853	6.351
	Bole (plus bark) (kg)	8.950	14.9.9	19.527	25.353	34.862	50.516	56.918	67.115
	Cones (kg)	1.982	.606	.493	.500	1.772	1.305	.800	.218
	Dead branches (kg)	-	-	-	-	-	-	-	-
	Total (excl. dead branches (kg)	12.603	18.015	24.187	32.078	44.074	60.719	68.944	80.438
	Foliar nitrogen (gm)	12.04	21.04	20.03	36.68	41.98	40.95	56.19	99.16
	Foliar phosphorus (gm)	1.140	1.707	1.819	3.026	3.461	3.503	4.593	7.488
14½	D.B.H.O.B. (in)	5.36	6.14	6.32	6.66	7.14	7.36	8.20	8.66
	Foliage (kg)	2.77	2.58	3.38	3.71	5.64	3.08	11.01	10.77
	Branch (kg)	3.37	3.85	5.51	9.02	8.89	7.77	16.45	17.46
	Bole (plus bark) (kg)	34.82	38.11	39.15	57.25	72.27	68.99	93.18	90.83
	Cones (kg)	-	1.31	.41	1.13	2.17	1.04	1.42	1.17
	Dead branches (kg)	0.52	0.61	1.01	1.80	1.10	2.01	1.14	2.34
	Total (excl. dead branches) (kg)	40.97	45.96	48.45	71.10	88.97	80.88	122.06	120.22
	Foliar nitrogen (gm)	34.97	27.35	45.20	39.30	64.02	32.66	140.42	128.44
	Foliar phosphorus (gm)	3.156	2.663	4.726	4.217	6.332	3.688	13.529	13.654
17½	D.B.H.O.B.	4.57	5.36	5.50	5.90	6.86	7.18	8.14	8.50
	Foliage (kg)	1.14	0.92	1.32	1.98	4.07	2.50	4.67	6.94
	Branch (kg)	1.64	1.46	2.24	2.93	8.45	4.74	7.54	16.39
	Bole (plus bark) (kg)	37.28	43.41	42.22	68.60	80.95	78.58	98.61	123.91
	Cones (kg)	1.63	1.92	3.17	1.20	1.80	2.44	5.67	1.35
	Dead branches (kg)	1.48	0.24	3.10	3.57	5.96	6.05	7.11	4.43
	Total (excl. dead branches) (kg)	41.70	47.71	48.95	74.71	95.26	88.36	116.49	149.13
	Foliar nitrogen (gm)	13.75	9.95	14.76	210.76	53.14	37.84	58.43	75.58
	Foliar phosphorus (gm)	1.420	1.107	1.553	2.189	4.408	3.880	5.084	7.556

	Weight in kg.	
Foliage	7.426	
Branch	9.783	
Bole	21.633	
Cones	0.203	(average of 8 trees)
Total	39.045	

The component weights calculated by regression and the total weight obtained by summation of components are close to what would have been expected from inspection of tree data in Table 4.3. Moreover, the regression-derived weights are probably underestimates of the various components. It was decided therefore to base the plot data on the regression equations.

For all four plots, the weight of the tree components was derived by solving the equations for each diameter class using the stand tables, and summing the data for these. Total plot weight was obtained by summing the component tree weights. The weight of cones and dead branches was estimated by multiplying the mean for the eight trees by the number of trees per plot.

The dry weight production in kilograms per hectare (kg./ha.) for each plot is summarised in Table 4.4 and illustrated graphically in Fig. 4.3. Changes in percentage distribution of the aboveground components with time are illustrated in Fig. 4.4.

Between 7½ and 14½ years, total dry weight contained in tree components increased from 46.31 to 124.13 x 10^3 kg. per ha. Most of this is associated with increase in bole weight (25.7 to 102.7 x 10^3 kg./ha.). In the same period canopy weight (branches plus foliage) actually declined from the peak recorded at 7½ years, when canopy weight was 20.4 x 10^3 kg./ha. made up of 11.6 x 10^3 kg. branches and 8.8 x 10^3 kg. foliage per hectare.

Both branch and foliage weight have apparently been strongly influenced by spacing. On the close-spaced plots (11½ and 17½ years), total canopy weights were 12.46 and 11.83 x 10^3 kg./ha. respectively i.e., about half the canopy weight in the 7½-year plot; and foliage weights were 5.65 and 4.09 x 10^3 kg./ha. respectively i.e., nearly half the foliage weight

Table 4.4

Dry weight of tree components per unit area of *P.radiata* forest for the an age sequence at Kowen (A.C.T.)

(unit = 1000 kg./ha.)

Component	Stand age (years)			
	7½	11½	14½	17½
Foliage	8.81	5.65	6.27	4.09
Branches	11.60	6.91	9.92	7.74
Bole (plus bark)	25.66	47.74	76.84	102.69
Cones	0.24	1.44	1.31	3.59
Dead branches	-	*	2.00	6.02
Total (including dead branches)	46.31	61.74	96.34	124.13

* Pruned to 8 ft.

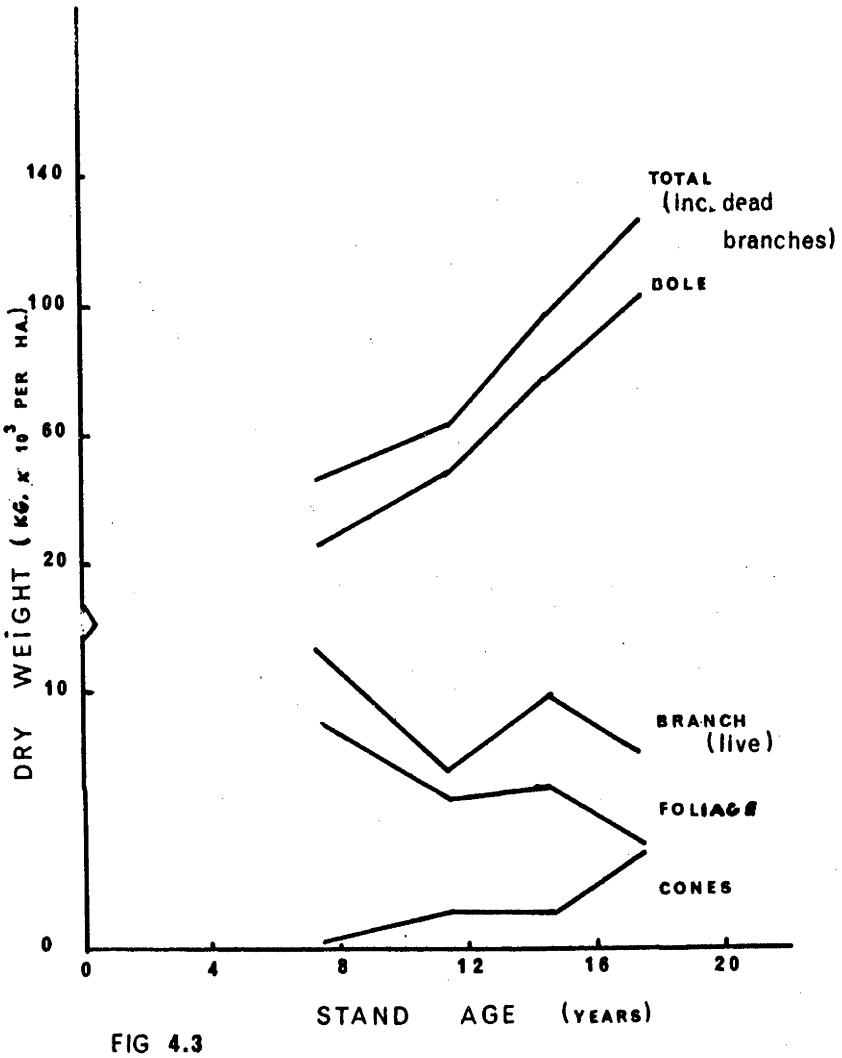

FIG 4.3

Variation in the dry weight of tree components with stand age in a low quality P. radiata forest (Kowen, A.C.T.)

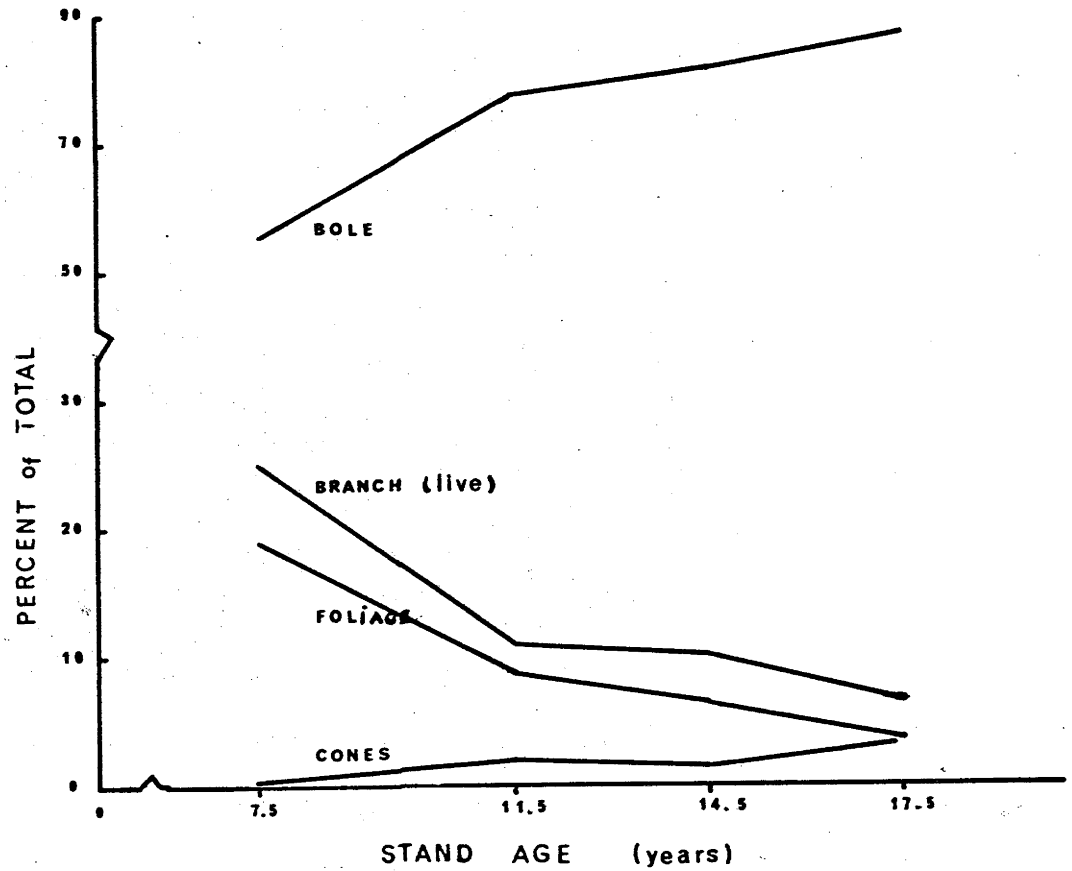

FIG 4.4

Variation in the percentage distribution of above ground tree components with stand age in a low quality P. radiata forest (Kowen, A.C.T.).

of the 7½-year-old plot. When the stands of similar stocking are compared (7½ yrs, 14½ yrs) decline in foliage and branch weight is still apparent but not nearly as marked. At 14½ years, foliage weight was 6.3 x 10^3 kg./ha. (8.8 at 7½ years), and branch weight was 9.9 x 10^3 kg./ha. (11.6 at 7½ years).

With increasing stand age, contribution of the canopy (branches and foliage) to total above ground weight declines rapidly (Fig. 4.4) e.g., at 7½ years the foliage represents nearly 20 per cent of stand weight, at 11½ years - 9 percent, at 14 years - 7 per cent and at 17 years - 3 per cent. The decline in total foliage weight between 7½ and 11½ years, both in absolute terms and as a percentage of stand weight, is striking. This decline cannot be attributed to a rise in green crown level resulting from crown closure. There were no dead branches on the 11½-year plot and at the spacing of this plot (610 stems per acre) crown closure takes place at about 12 years. This suggests that on the Kowen site, competition between crowns may seriously affect crown vigour well before crown closure takes place, and this influence on crowns may be more serious on close-spaced than on wide-spaced plots. The 11½-year plot carried 610 stems per acre, and total crown production had been adversely affected over a 4-5 year period prior to crown closure. Dead branches were recorded in the wider-spaced 14½-year plot but were a more pronounced feature of the 17½-year plot where weight of dead branches was not much less than weight of live branches, and in fact exceeded foliage weight. As expected, cone production per acre rose slowly with age.

4.3.2 Distribution of stand foliage in 1-year to 4-year needles

The distribution of the total foliage dry weight in 1-year, 2-year, 3-year and 4-year needles respectively has been analysed for each plot. At 7½ years only 20 per cent of the total foliage dry weight was in 1-year needles while the percentages in 3- and 4-year needles were 28 and 36 per cent respectively, that is, at 7½ years the greatest proportion of total foliage was in the 4-year needles. By contrast, the relative distribution of foliage dry weight was reversed at subsequent

ages; at 11½ , 14½ and 17½ years the greater proportion of foliage dry weight was in 1-year needles (30 - 35 per cent) while that in 2-year needles was 21-25 per cent, 3-year needles 24 - 29 per cent, and 4-year needles 14 - 21 per cent (see Table 4.9).

In any one year, the amount of foliage produced is related in part to environmental conditions during the growing season; for example, the weight of 2-year needles is low in all stands (Table 4.9). Nevertheless, in the 7½-year stand, the marked decline in needle weight from 4-year to 1-year needles suggests annual production of new foliage on this low quality site might be a maximum as early as 4 years. Moreover, it is expected that some translocation of materials would take place from needles between their production in year 1, and years 3 and 4, so that present weight of 3 and 4-year needles must be an underestimate of new needle production when the 7½-year stand was 5½ and 4½ years old respectively.

When absolute needle weights are plotted as an increasing age series (years 4 to 17 - Fig. 4.5), the following features are apparent:

(1) Production of needles in years 4 and 5 (i.e., the 4-year and 3-year needles in the 7½-year stand) would have been greatly in excess of that in all subsequent years. Actual new needle weight in years 4 and 5 would in fact be greater than absolute weights shown because of translocation.

(2) Current needle production was more or less stable over the age range 7 - 17 years, with slightly greater production in the wider spaced plots. Nevertheless, production of these plots would still be well below probable production levels at stand ages of 4 and 5 years.

(3) In the wide-spaced plot (14½ years) weight of 3-year needles is approximately equal to that of current needles. By contrast, weight of 3-year needles in high density plots is less than that of current needles. This could be an environmental effect, or, alternatively,

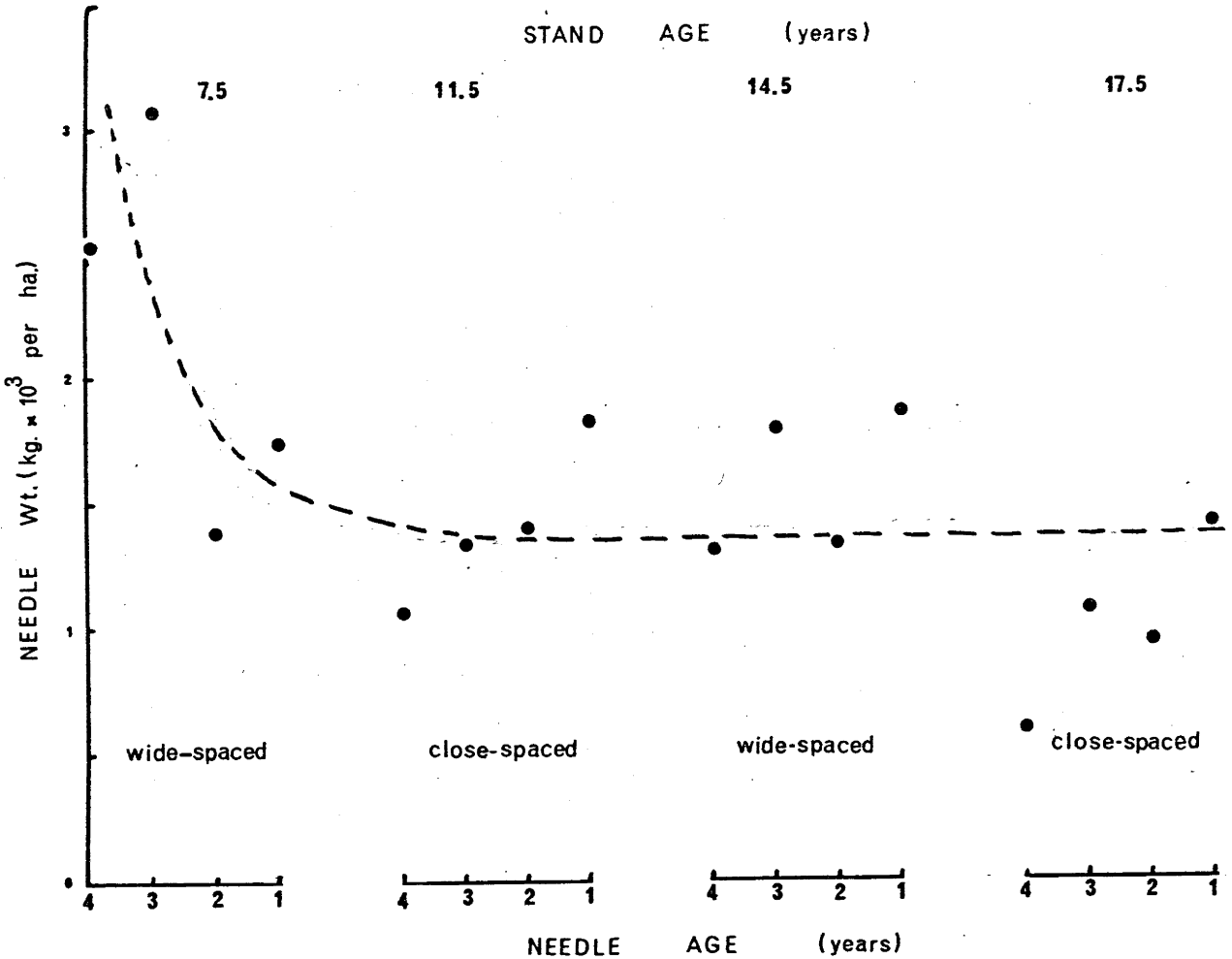

FIG 4.5

Needle weights produced over an age sequence of 4-17 years in a low quality P. radiata forest. (Data are needle weights, aged 1-4 years respectively in age sequence of stands 7½, 11½, 14½ and 17½ years of age).

translocation in high density plots could be greater than on plots where competitive stress is lower.

In summary, the principal features of foliage production with age on the low-quality site are as follows:

(a) Peak foliage production apparently occurs at about 4 years of age;

(b) A sharp decline in foliar production occurs thereafter, that is, long before canopy closure which occurs at about 12 years on this site;

(c) New foliage production is relatively constant from 7½ - 17½ years, with the qualification that stand density affects foliage production;

(d) Loss of needle weight by translocation between year 1 and 3 may be small, i.e., translocation may be restricted in trees on a poor quality site.

4.3.3 Discussion

On the low quality Kowen site, peak annual foliage production is probably achieved long before canopy closure, while at Tumut, N.S.W., on a more productive site, peak foliage production is associated with canopy closure (Forrest, 1969). There seems to be two possible explanations for the foliage production pattern at Kowen:

(i) site factors are in limited supply and their maximum use is achieved very early in stand development; and

(ii) after about 4 years of age there is a radical change in the distribution of total site production to the various tree components (boles, branches, foliage) i.e., after 4 years, an increasingly larger proportion of dry weight production is in bole wood.

It is possible that both factors contribute to the Kowen production pattern.

The apparent strong influence of stocking on foliage weight shown over the age range suggests maximum site use may be achieved very early, and that on this site there is only a narrow range of stand density over which there is a constant

and maximum level of foliage production. It is generally accepted that for most species there is, at a given age, a fairly wide range in stand density over which both wood volume and foliage weight are constant (Möller, 1947). Satoo (1967) has even shown that foliage weight of Pinus densiflora is relatively independent of both stand age and site quality over a wide range of both. In these terms, a stocking of 610 stems per acre or 94 sq. ft basal area per acre at 11½ years on the Kowen site may represent a stand density beyond the range at which foliage weight is constant; it may represent a point at which average tree "efficiency" is falling, and full site use is not achieved. In any stand, part of the site capacity is available for continuing dry matter production, and part is used for "maintenance" of the stand already produced (Lewis, 1959). Beyond a certain stand density, that part of the site capacity orientated to "stand maintenance" increases and that orientated to foliage and wood production decreases.

Despite the decline in crown weight of P.radiata on the Kowen site after 7½ years, total above ground biomass continues to increase i.e., an increasing proportion of the total site production is directed to bole wood. The species has been able to maintain production of bole wood despite declining crown weight. This could be one reason for its high productivity over a wide range of sites in Australia. However, on the low quality Kowen site, weight of bole wood per unit foliage weight is very similar to that of the better quality Tumut site within the common range examined (Table 4.5).

Table 4.5

Ratios of bole weight and branch weight to foliage weight at Tumut and Kowen sites:

Stand age (years)		3	5	7	9	12
TUMUT	Bole:foliage	0.82	1.23	2.13	5.43	9.73
	Branch:foliage	0.39	0.63	1.33	1.18	2.03
	Total	1.21	1.86	3.46	6.61	11.76
Stand age (years)		7½	11½	14½	17½	
KOWEN	Bole:foliage	2.91	8.45	12.26	25.11	
	Branch:foliage	1.32	1.22	1.58	1.89	
	Total	4.23	9.67	13.84	27.00	

For example, the following data are bole weight:foliage weight ratios at Tumut and Kowen respectively derived from Table 4.5:

Bole:foliage weight	Age (years)				
	7	7½	9	12	13
TUMUT	2.13		5.43	9.73	
KOWEN		2.91	5.68*		10.35**

* 5.68 is the mean of ratios at 7½ and 11½ years

** 10.35 is the mean of ratios at 11½ and 14½ years

Within the range 7-13 years, the ratio of bole weight: foliage weight rises and the pattern of change in the ratio is similar for both Kowen and Tumut sites. At 17½ years on the Kowen site, the ratio had risen to 25.11, but comparable data for Tumut are not available. These data suggest, at least, that despite the difficult environmental conditions at Kowen, the total foliage is no less efficient in producing bole wood than at Tumut;

a given amount of foliage is producing similar bole wood at both sites and the amount changes in a regular pattern with age on both sites.

4.4 RESULTS II : ACCUMULATION AND DISTRIBUTION OF N AND P IN FOLIAGE

4.4.1 Accumulation of foliar N and P

Sample tree foliage was analysed for nitrogen and phosphorus. Altogether 18 tree strata/needle age samples were analysed for each of the 32 trees. The 18 samples were made up of 1, 2 and 3-year old needles respectively in the 1, 2 and 3-year tree strata; and 4 needle ages in each of the 4-5 year, 6-7 year, and 7 year plus tree strata.

Total weight of nitrogen and phosphorus in the foliage of each sample tree was calculated from the weight of needles in each tree stratum/needle age unit, and the corresponding foliar percentages of nitrogen and phosphorus.

Regression equations of the form:

$$\underset{\text{(gm)}}{\text{Log}_e\ (\text{Nutrient weight})} = b \times \underset{\text{(sq.ft)}}{(\text{basal area})} + a$$

were calculated for each plot using 8 sample trees (Table 4.6). Regression equations were solved for each diameter class in a plot and the total of all classes summed to give total foliage nutrient weight for the plot.

All regression equations were significant except that for the 7½-year stand. When the D.B.H. of each sample tree is plotted against its $\log_e$ (total foliar N weight) and $\log_e$ (total foliar P weight) respectively, the weights of both N and P in the foliage are seen to be nearly constant for stems above 4.00 in. d.b.h. and to decline sharply for stems below 4.00 in. d.b.h. (Fig. 4.6). Consequently, derivation of the total foliar nutrient content on this plot has been based on the following:

(a) for trees > 4.00 in. d.b.h., the average nutrient content (N and P) of six sample trees was multiplied by the number of trees in the plot; and

Table 4.6

Regression equations relating weight (gm) in the foliage with tree basal area (sq. ft) in the form of : Log_e (Nutrient weight) = b x B.A. + a

Stand age (years)	Nutrient weight in the foliage	b	a	r	Significance of r
7½	Nitrogen	*	*	*	N.S.
	Phosphorus				
11½	Nitrogen	8.8668	+ 2.3059	.834	$p < 0.01$
	Phosphorus	8.6809	- 0.0796	.844	$p < 0.01$
14½	Nitrogen	6.2748	+ 2.2708	.742	$p < 0.05$
	Phosphorus	6.6108	- 0.1080	.780	$p < 0.05$
17½	Nitrogen	7.7537	+ 1.3443	.769	$p < 0.05$
	Phosphorus	6.5212	- 0.5437	.829	$p < 0.05$

* Regression not used: see p. 94-5 for explanation.

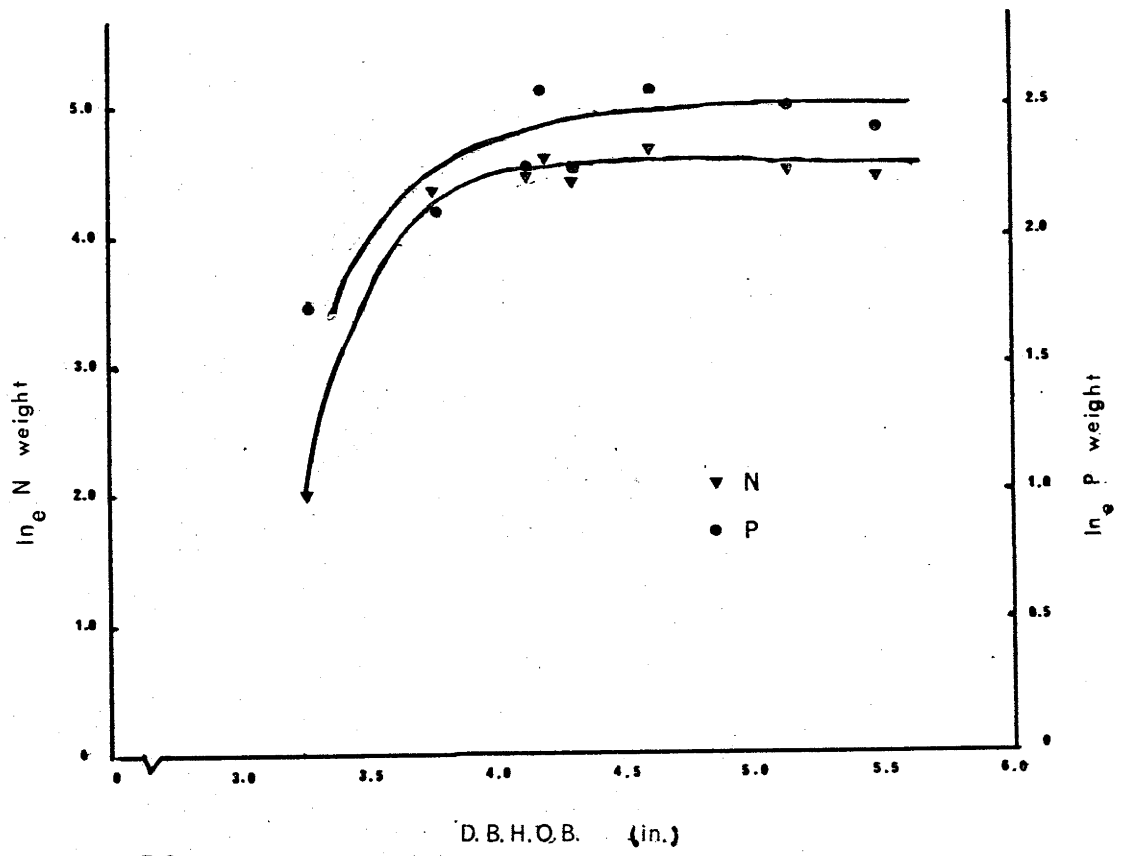

FIG 4.6

Relationship between tree diameter and total weights of N and P in the foliage of a 7½-year stand on a low quality site (Kowen, A.C.T.).

(b) for trees < 4.00 in. d.b.h., the regression equation established by the two smallest sample trees was used.

The weight of nitrogen contained in the foliage of the four plots was at a peak in the 7½-year-old stand (Table 4.7). When compared with the stand of similar spacing (4½-year plot), total foliage nitrogen is seen to have declined from 99.8 to 59.0 kg./ha. The more heavily stocked plots (11½-year and 17½-year plots) contained 46.7 and 33.8 kg./ha. of nitrogen respectively in their foliage, that is, less than half the weight of nitrogen in the 7½-year plot. The nutrient weight in the 11½-year plot has been adjusted for pruned material as described previously. The adjusted weight is probably an overestimate since foliar N and P content tends to decline at the base of the crown (refer Section 4.4.2).

On this low-quality site, therefore, heavy stocking has led to a marked reduction in both total foliage weight and in the total foliage nitrogen. The phosphorus pattern with age is similar to that of nitrogen viz., a sharp decline from 12.36 kg. per ha. at 7½ years to 5.96 kg. per ha. at 14½ years. In the more heavily stocked plots, weight of foliage phosphorus was only 5.13 kg. per ha. at 11½ years and 3.86 kg. per ha. at 17½ years.

Forrest (1969) calculated total foliage phosphorus content for a higher quality stand at Tumut, N.S.W. (Table 4.7). At 7 years, his stand contained 14.26 kg. of phosphorus per ha. in foliage; that is, the stand had a mean annual increment of 2.04 kg. per ha. per year. The foliage phosphorus in the Kowen stands was not much less at 7½ years (12.36 kg./ha.); that is, this stand had a mean annual increment of 1.65 kg. per ha. per year. Beyond seven years, the Tumut stand contained 13.54 kg./ha. at 12 years i.e., slightly less than it did at 7 years. Consequently, the mean annual increment falls to 1.13 kg. per ha. per year. At Kowen, total foliage phosphorus was only 5.13 kg./ha. at 11½ years i.e., less than half the weight at 7½ years. Thus, at 11½ years, the mean annual phosphorus increment in the foliage at Kowen was only 0.45 kg. per ha. per year.

On the moderately high quality site at Tumut, Forrest (loc.cit.) found that peak foliage weight and maximum accumulation

Table 4.7

Nutrient weight in the foliage of P.radiata in four stands over the age range 7½ to 17½ years (Kowen Forest)

Nutrient weight (kg./ha.)	Stand age (years) 7½	11½	14½	17½
Nitrogen	99.78	46.72	58.98	33.76
Phosphorus	12.356	5.132	5.958	3.858
Foliage dry weight as per cent of total tree weight above ground	19.4	9.1	6.6	3.2

Nutrient weight in the foliage of P.radiata at Tumut (S.Q III) (Data from Forrest, 1969)

Nutrient weight (kg./ha.)	Stand age (years) 3	5	7	9	12
Phosphorus*	0.568	2.45	14.26	9.39	13.54
Foliage dry weight as per cent of total tree weight above ground	49.5	37.0	22.9	11.9	8.0

* Nitrogen data are unavailable for the Tumut site.

of foliage phosphorus was associated with canopy closure i.e., about 7 years of age in a stand planted at 8 x 8 ft spacing (680 stems per acre). On the low quality Kowen site, both peak foliage weight and accumulation of foliage occurred well before canopy closure. At Kowen, canopy closure occurs at about 12 years in a stand carrying 610 trees per acre, but between 7½ and 11½ years of age both foliage weight and phosphorus weight in the foliage declines sharply. Extreme competition between individuals on the Kowen site is clearly having an adverse effect on the crown vigour and canopy development of heavily stocked stands by or soon after 7½ years. Needle production has probably reached a peak at or before 4 years. On such sites, maximum site use is achieved well before canopy closure, and once this is achieved, continuing production of foliage and uptake of phosphorus is severely restricted. By contrast, foliage weight and foliage phosphorus did not decline appreciably after canopy closure in Tumut stands.

In view of the difference between Tumut and Kowen stands in the period 7 - 12 years, the comparability of the stands at 7 years may seem surprising. The rapid development of foliage and uptake of phosphorus up to 7 years at Kowen may be due in part to the pre-planting ripping of the soil at Kowen. This was not carried out at Tumut, and, furthermore, early tree growth at Tumut may be affected by competition from weed species and restricted mineralisation of organic nitrogen and phosphorus in the largely undisturbed soil. At Kowen, ripping ensures a more rapid utilisation of site potential, but full site use is achieved very early and continuing growth leads to a rapid decline in foliage production. Nevertheless, despite the reduction in foliage weight, bole wood production remains at a commercially acceptable level; on this site the mean annual increment at 20 years would probably be of the order of 175 cubic feet per acre per annum.

4.4.2 Variation in foliar N and P content

On the low production site at Kowen, full utilization of site factors is apparently achieved at a very early stage of stand

development. Thereafter, foliage weight per acre and weight of nitrogen and phosphorus contained in foliage decline although the weight of new foliage produced each year is fairly constant.

It now remains to examine the distribution of nitrogen and phosphorus within the tree foliage on the low quality site, and to compare this with the distribution of phosphorus within the tree foliage on the better quality Tumut site.

Patterns of foliar nitrogen and phosphorus concentration on the Kowen site were examined in terms of the influence of tree size, tree age, crown position, and needle age.

(a) Influence of tree size on foliage nutrient content

Data for each stand were examined to determine whether there is any relationship between tree size and foliar nitrogen and phosphorus content respectively. Within the one stand, tree size and foliar nitrogen and phosphorus percentage are unrelated. Correlation coefficients of the relationships between $\log_e N$ per cent and $\log_e P$ per cent respectively with $\log_e$ (tree diameter) are not significant. This result is similar to that obtained by Forrest (1969). Consequently, for a given crown position, the mean foliar concentration for the eight sample trees in any one plot can be accepted as a representative value for the plot.

(b) Influence of tree age on foliar nutrient content

An analysis was made testing whether foliar nutrient levels at a standard crown position differ between the four stands within the age series. Differences between mean foliar nitrogen percentage in 1-year needles on the 1-year whorl were not significant (Table 4.8) although the mean N per cent at 11½ and 14½ years (1.17 and 1.18 per cent respectively) are lower than those recorded at 7½ and 17½ years (1.26 and 1.31 per cent respectively).

By contrast, differences between phosphorus levels at the standard sampling position are significant ($P < 0.01$) and, again, the phosphorus levels at 11½ and 14½ years (0.138 and 0.166 per cent respectively) are well below those at 7½ and 17½ years (0.290 and 0.195 per cent respectively).

This pattern of variation in phosphorus per cent with stand

TABLE 4.8

Variation of Foliar N and P content with Tree Age, Needle Age and Crown Position and that of N : P Ratio with Stand Age in P. Radiata at Kowen (A.C.T.)

		N per cent					P per cent				
Stand Age[1] (years)		$7\frac{1}{2}$	$11\frac{1}{2}$	$14\frac{1}{2}$	$17\frac{1}{2}$		$7\frac{1}{2}$	$11\frac{1}{2}$	$14\frac{1}{2}$	$17\frac{1}{2}$	
	Mean	1.26	1.18	1.17	1.31		.290	.138	.166	.195	
	Analysis of variance	N.S.					Sign P < 0.01				
	L.S.D.[2]						.154 for P < 0.05				
Needle Age[3] (years)		1	2	3	4		1	2	3	4	
	Mean	1.21	1.14	1.20	1.12		.175	.131	.128	.126	
	Analysis of variance	N.S.					Sign P < 0.01				
	L.S.D.[2]						.013 for P < 0.05				
Crown Position[4] (whorl age — years)		1	2	3	4	6-7	1	2	3	4	6-7
$7\frac{1}{2}$yr stand:											
	Mean	1.26	1.16	1.22	1.21	1.03	.292	.258	.226	.175	.173
	Analysis of variance	Sign. P < 0.05					Sign. P < 0.01				
	L.S.D.	0.10					.040				
$17\frac{1}{2}$yr stand:											
	Mean	1.31	1.27	1.24	1.23	1.21	.166	.170	.149	.148	.144
	Analysis of variance	N.S.					N.S.				
	L.S.D.										
N : P Ratio[5] variation with stand age		N per cent : P per cent					N weight : P weight				
	Stand Age (yrs)	$7\frac{1}{2}$	$11\frac{1}{2}$	$14\frac{1}{2}$	$17\frac{1}{2}$		$7\frac{1}{2}$	$11\frac{1}{2}$	$14\frac{1}{2}$	$17\frac{1}{2}$	
	Mean ratio	4.50	8.78	6.25	8.23		7.76	11.91	9.74	9.99	
	Analysis of variance	Sign. P < 0.01					Sign P. < 0.01				
	L.S.D.	2.34 for P < 0.05					1.50 for P < 0.05				

Notes:
1 = 1-yr needles on the first lateral whorl
2 = Tukey's multiple range
3 = needles in 4-5 yr whorl for $7\frac{1}{2}$-yr stand; the pattern is the same for all four stands
4 = the pattern for $11\frac{1}{2}$-yr and $14\frac{1}{2}$-yr stands is similar to that of $17\frac{1}{2}$-yr stand
5 = the ratio has been calculated from (a) N per cent : P per cent and (b) Total N weight to total P weight in the foliage

age differs from that of a site quality III stand (Forrest, loc. cit.) where phosphorus per cent tended to increase irregularly with stand age. Forrest regarded the relatively stable phosphorus level as reflecting an adequate supply to the trees through the age range 3 - 12 years which includes canopy closure and the period of maximum accumulation of dry matter and phosphorus. If this is in fact the case, then on the low quality Kowen site, the very marked decline in foliar phosphorus between 7½ years, and 11½ and 14½ years may reflect a developing stress condition for phosphorus and this may be associated with the severe within-stand competition on this site after 7½ years. The subsequent increase in the concentration of foliar phosphorus at 17½ years may reflect some amelioration of the P-stress condition following the phase of peak demand on soil phosphorus by the stand. It may also reflect a concentration of phosphorus accumulation as total foliage weight declines. While the more marked fluctuation in foliar nutrient is in phosphorus content, the fluctuation in foliar nitrogen follows a similar pattern but is not great enough to give a significant stand age difference.

The difference in the extent of fluctuation of nitrogen and phosphorus per cent is reflected in the N : P ratio over the stand age series. This changes from 4.5 at age 7½ years to 8.8 at 11½ years, 6.3 at 14½ years and 8.2 at 17½ years. The difference between these means is significant ($P < 0.05$). A similar age-pattern of change in the N : P ratio was obtained using total weight of nitrogen and phosphorus in the whole crown foliage; these were 7.8, 11.9, 9.7 and 9.9 for ages 7½, 11½, 14½ and 17½ respectively. The difference between 7.8 and 11.9 is again significant at $P < 0.05$. Between 7½ and 11½ years, when severe between-tree competition is established on this site, the N : P ratio rises significantly. While both foliar N and P levels decline, the drop in foliar P is greater than that of foliar N. This suggests a relatively greater P-stress than N-stress developing between 7½ and 11½ years, although the very high foliar P level at 7½ years may indicate excess or luxury uptake of P up to 7½ years, but this does not apply to nitrogen. This pattern is similar to that of the younger Mt Burr stands

described in Chapter 2.

(c) Influence of crown position on foliar N and P content

The influence of crown position on foliar N and P has been analysed for the youngest (7½ years) and oldest (17½ years) stands in the age series (Table 4.8). In the youngest stand, foliar nitrogen in 1-year needles is constant through the 1-year, 3-year and 4-5 year whorl strata of the tree (1.26 - 1.21 per cent) but the percentage N in the 6-7 year whorl stratum is lower (1.03 per cent). By contrast, the P percentage declines progressively from a high of 0.292 per cent in the 1-year whorl to around 0.175 per cent in the 4-5 and 6-7 year whorls.

In the oldest stand (17½ years), canopy position does not have a significant effect on either nitrogen or phosphorus content in 1-year needles, although there is a trend for the content to be a maximum in the youngest whorl (1-year) in the crown.

The influence of canopy position on foliar phosphorus in the low quality Kowen forest differs from that described by Forrest (1969) for the higher quality Tumut stand at least at and after canopy closure. At Tumut, foliar P, K, Mg and Zn decreased with increasing distance from the tree apex. However, at each crown position, the foliar concentration given by Forrest is the value for the total foliage at that location i.e., for material of increasing average age down the crown. Nevertheless, it seems possible that a more or less constant nutrient level in 1-year needles over the whole crown may be a characteristic of trees on low quality but not on higher quality sites.

(d) Influence of needle age on foliar nutrient content

The influence of needle age on foliar nutrient content in the 4-5 year whorl-stratum within the canopy was examined in all four stands. The pattern of variation in foliar nitrogen and phosphorus with needle age was similar for all stands; consequently the results of only one analysis (7½-year-old stand) are presented in Table 4.8.

Within the stratum sampled foliar nitrogen did not differ significantly with needle age. Mean foliar N per cent was 1.21

(1-year needles), 1.14 (2-year needles) and 1.20 (3-year needles). By contrast, there is a significant ($P = 0.01$) decline in foliar phosphorus content from 1-year to 2-year needles (0.175 to 0.131 per cent P). Thereafter, foliar P remains constant, being 0.128 and 0.126 per cent in 3- and 4-year needles respectively.

The pattern of variation in foliar nutrient content with needle age on the one whorl in the 7½-year stand is similar to the pattern of variation with distance from the tree apex in the same stand, that is, there is a phosphorus but not a nitrogen gradient. Foliar N remains more or less constant in needles aged 1-3 years while foliar P declines steeply between 1- and 2-year needles. In addition, foliar N is more or less constant over the whole age stratum of the tree in contrast to foliar P.

Over the needle age range 1-3 years, there is no consistent gradient in foliar N (e.g. 1.21, 1.14 and 1.20 per cent for 1-, 2- and 3-year needles respectively) and this is the case for all four Kowen stands. The distribution of phosphorus within the Kowen stand compared with that of nitrogen can be further emphasized by comparing the percentage of total N and P accumulated in the stand foliage which is contained in one-year needles:

	Percentage of total stand foliage nutrients in one-year needles:			
Stand age (years)	7½	11½	14½	17½
Phosphorus	30%	39%	38%	43%
Nitrogen	22%	30%	29%	37%

More of the total foliar P is contained in current needles than total N (see also Table 4.9).

Table 4.9

Percentage distribution of foliage dry matter, weight of foliar nitrogen and weight of foliar phosphorus in 1-year, 2-year, 3-year, and 4-year 4^+ needles

Stand age (years)	Needle age (years)	Dry matter	Nitrogen weight	Phosphorus weight
7½	1	19.5 ± 1.8	22.3 ± 2.5	29.8 ± 2.2
	2	15.8 ± 1.3	17.0 ± 1.2	15.8 ± 1.1
	3	35.8 ± 3.1	34.8 ± 3.3	30.0 ± 2.6
	4+	28.7 ± 1.9	25.9 ± 2.9	24.5 ± 2.2
11½	1	32.8 ± 3.6	30.4 ± 3.8	39.1 ± 3.6
	2	24.7 ± 1.6	25.6 ± 1.4	23.6 ± 1.4
	3	23.6 ± 1.8	24.9 ± 2.0	21.8 ± 1.8
	4+	18.9 ± 1.5	19.0 ± 1.7	15.6 ± 1.6
14½	1	30.0 ± 3.4	29.1 ± 2.7	38.2 ± 2.8
	2	21.4 ± 0.9	23.9 ± 1.3	21.9 ± 1.2
	3	28.8 ± 2.0	31.8 ± 2.7	27.4 ± 2.1
	4+	20.9 ± 3.5	15.0 ± 2.8	12.5 ± 2.3
17½	1	35.1 ± 2.2	37.2 ± 2.5	43.1 ± 2.9
	2	23.3 ± 1.7	25.0 ± 1.9	22.4 ± 1.3
	3	26.5 ± 2.3	24.9 ± 2.6	22.7 ± 1.9
	4+	15.0 ± 3.0	13.0 ± 2.4	11.9 ± 2.3

4.4.3 Discussion

The nutrient status of the trees on the Kowen site over the age range studied (7½ to 17½ years) can be characterised by the three foliar nutrient indices:

(a) nutrient concentration in 1-year needles at a standard sampling point;

(b) the vertical concentration gradient within the crown; and

(c) the horizontal gradient in the crown.

(a) Nutrient concentration in 1-year needles at a standard sampling point

The nitrogen and phosphorus concentration in current needles might be interpreted as follows: Phosphorus concentration at 7½ years was very high (0.290 per cent). This suggests there was a relatively large pool of available phosphorus following removal of indigenous vegetation and site preparation. Largely because of site preparation (cultivation), the tree root systems were able to explore the limited soil volume quickly. By 7½ years, the Kowen site was able to accumulate a weight of phosphorus that was not much less than that of the more productive Tumut stand at 7 years. However, in contrast to Tumut, percent phosphorus at Kowen dropped sharply at 11½ years, and this may reflect the development of a phosphorus stress condition. On this site, complete site utilization occurs very early and, thereafter, the rate of phosphorus availability from the soil may slow down appreciably.

Pinus radiata has a rapid early growth phase, current annual basal area and volume increment reaching peaks around 6-8 years and 10-12 years respectively. It seems, therefore, that the large foliar P content at 7½ years is used to maintain bole wood production during this critical part of the rapid growth phase when the rate of supply from the soil is low. Foliage weight is reduced and phosphorus in the foliage is probably relocated in maintaining bole wood production. Thereafter, the rate of soil supply may be better able to meet the demand, and the foliar phosphorus concentation again rises.

The differences in foliar nitrogen content in current needles over the stand age range examined were not significant, but the trend was similar to that of phosphorus.

(b) The vertical concentration gradient within the crown

An important feature of the vertical foliar nutrient concentration gradients on the Kowen site is the contrast with the Tumut site. At the Kowen site, there was no regular pattern in either the 7½ or 17½ year old stands examined. There was no phosphorus gradient in the 17½ year stand, although there was a trend for the percentage to be a maximum in the youngest (1-year) whorl. At Tumut, foliar nitrogen was not examined but foliar levels of P, K, Mg and Zn decreased with increasing distance from the tree apex. It is suggested that the steep vertical phosphorus gradient in the 7½-year stand at Kowen may reflect a still relatively vigorous condition of the trees only a few years after the presumed full site utilization had been achieved resulting in translocation of a large amount of phosphorus to the growing shoots. Alternatively, the lack of any vertical gradient in the 17½-year stand could reflect the limiting site factors, the high density of stocking, and the low vigour of the trees on the Kowen site beyond the age of 7½ years. As in Chapter 2, differences in the nature of the vertical concentration gradient between stands again suggest that translocation activity in trees of low vigour may be weak. The effects of low site quality on translocation within trees are examined in Chapter 5.

(c) The horizontal concentration gradient within the crown

A horizontal gradient i.e., decreasing nutrient concentration with needle age in the one whorl, occurs for phosphorus only in all four stands. This gradient is characterised by a steep drop from year 1 to year 2 needles and relative stability thereafter. The pattern is similar to that of the "Sands" in the south-east of South Australia, and may indicate some phosphorus stress on the site. The lack of a regular needle age/foliar nitrogen gradient is puzzling; in this respect, these stands are unlike those of all the South Australian sites examined. Possibly,

the absence of a needle age gradient could reflect a large supply of nitrogen relative to phosphorus or limited translocation of nitrogen within the tree crown. The latter suggestion seems more likely because of the low foliar N:P ratios in the four stands (Table 4.8). An attempt to solve this question is made in Chapter 5.

4.5 SUMMARY

The accumulation and distribution of foliage and foliar nitrogen and phosphorus in P.radiata were studied in an age sequence of stands (7½, 11½, 14½, and 17½ years respectively) on a poor site in Kowen in the A.C.T. The stocking of the stands ranged from 480-610 stems per acre.

The principal features of the production of foliage with age are as follows:

(1) peak foliage production apparently occurred at about age 4 years;
(2) a sharp drop of foliage weight occurred before canopy closure which is about 12 years of age on this site;
(3) production of new foliage was relatively constant from 7½ to 17½ years, with the qualification that stocking affects foliage production.

Within the age range of 7½-17½ years, the ratio of bole weight:foliage weight rose from 2.91 to 25.11. This rise is similar to that of a more productive stand reported by Forrest (1969), at least in the age range of 7-13 years.

At the age of 7½ years, P.radiata on this poor site contained as much as 99.8 kg./ha. of foliar nitrogen and 12.36 kg./ha. of foliar phosphorus; but thereafter the weight of these nutrients decreased to 33.8 and 3.86 kg./ha. respectively by age 17½ years.

Foliar nitrogen and phosphorus concentrations and patterns in tree crowns are influenced by tree age (especially during the peak demand period), crown position and needle age. Differences in these patterns are discussed.

CHAPTER 5

SEASONAL VARIATION OF FOLIAR NITROGEN AND PHOSPHORUS IN TREES OF VARYING VIGOUR

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5.1 INTRODUCTION

The vertical and horizontal gradients of foliar nitrogen and phosphorus concentration in P.radiata, examined in Chapters 2, 3 and 4, can be summarised as follows:

(a) In the plantation of south-east South Australia (Chapter 2), the foliar nutrient/needle age gradients, in the upper crown, particularly for P, are characteristic of different soil types. What does this gradient from current to older needles mean?

Firstly, it has been suggested that the horizontal gradient can be used to detect potential nutrient stress, the steeper the gradient the greater the possibility of nutrient stress developing, especially when deviations from an observed "normal" gradient are noted.

Secondly, the presence of a gradient from current to older needles could mean a better translocation of nutrients to actively growing tissues (see later).

(b) In four stands of varying vigour on two contrasted soils in the A.C.T. (Chapter 3), there were no differences between stands in the horizontal gradients of N and P with needle age; and although there was no vertical gradient of N and P in either of the low-vigour plots, there were vertical gradients of foliar N in the two vigorous plots on a single soil type.

(c) Within an age series on a low quality site in the A.C.T., the only vertical gradient recorded was for P in the youngest stand. In this age series, the youngest stand is the only one which could be regarded as still developing vigorously. The results of these studies suggested that the presence of strong gradients in foliar nutrients, especially the vertical gradient, might be correlated with stand vigour. An examination of the literature dealing with such gradients in tree crowns is summarised in Tables 5.1 and 5.2. These data do not indicate any inherent patterns of both foliar N and P concentration in tree crowns. This lack of patterns suggests that site may influence the internal distribution of N and P in the crown,

TABLE 5.1

Effect of Crown Position on Foliar Nutrients in Coniferous Forest Trees

Species	Age (years)	Increase toward apex	Increase toward base	Distribution pattern			References	Remarks
				Minimum in midcrown	Maximum in midcrown	No constant trend		
Abies alba (?)			Ca	K,Mg	P	N	Němec (1940)	healthy trees
Abies alba (?)		P	Ca,N			K,Mg	Němec (1940)	dying trees
Agathis australis			Ca,K	P		N	Peterson (1961)	
Taxus baccata			Ca,Mg	K,P			Němec (1947)	
Picea abies				K	N	Ca,Mg,P	Strebel (1961)	
Picea mariana		N					Gagnon (1964)	
Pinus elliottii						P	Humphreys and Kelly (1962)	
Pinus resinosa	12	K,N,P	Ca			Mg	White (1954)	K-deficient site
Pinus resinosa		K,P	Ca,K,P	K,P	Ca	Mg,N	Madgwick (1964)	poor and good sites
Pinus strobus	12	K,N,P	Ca			Mg	White (1954)	K-deficient site
Pinus sylvestris		K,N,P	Ca				Leyton and Armson (1955)	
Pinus teada		K,P	Ca,Mg,N				Well and Metz (1963)	
Pinus radiata			Ca	K,Mg,P		N	Will (1957)	
Pinus radiata	3-12	K,Mg,P,Zn	Ca,Mg				Forrest (1969)	good site
Pinus radiata	8	P				N	Present study	poor site
	17					N,P		poor site
	16					N,P		poor site
	14	N				P		good site

TABLE 5.2.

Effect of Increasing Needle Age on Foliar Nutrient Levels in Coniferous Forest Trees

Species	Age (Years)	Decrease	Increase	No Trend	References	Remarks
Agathis australis		K,N,P	Ca,Mn,Na,Si,Fe		Peterson (1961)	
Pinus elliottii	3-10	P			Humphreys and Kelly (1962)	P-deficient and non-deficient trees
Picea abies (?)	10-110	N,P	Ca,K,Si	Mg,Mn	Hohne (1963)	
Pinus resinosa	12	K,N,P	Ca,Mg	Mg	White (1954)	P-deficient sites
Pinus resinosa		K,N,P			Heiberg et al. (1958)	
Pinus resinosa		K,N,P	Ca	Mg	Madgwick (1964)	
Pinus sylvestris		K,N,P	Ca,Na		Ovington (1959)	
Pinus sylvestris		K,N,P	Ca	P	Leyton and Armson (1955)	
Pinus sylvestris		K,N,P,Na			Madgwick (1962)	
Pinus radiata		Mg,N,P (at crown top)	Ca,Na,P (at crown base)	K	Will (1957)	
Pinus radiata		P			Askew (1937) Manshard (1933)	
Pinus radiata	4	K,N,P			Raupach (1963)	K-deficient and non-deficient trees
Pinus radiata	7-17	P		N	Present study	poor site
	14	N,P			Present study	good site

possibly through differences in translocation. This hypothesis is tested in the present chapter.

Outward movement of minerals from leaves seems to be related to outward movement of carbohydrates (Rutter, 1957; Kozlowski and Winget, 1964; Taylor, 1967; Kozlowski and Keller, 1966; Krueger, 1967; Dickman and Kozlowski, 1968). The relative amounts of seasonal fluctuation in the nitrogen content of leaves, twigs, bark and wood have been observed in many trees and are probably of universal occurrence (Kramer and Kozlowski, 1960). In autumn, a considerable part of the nitrogen and minerals in leaves is translocated into the twigs before abscission occurs.

Some of the earlier studies of translocation are suspect because it was not shown that nitrogen moved back into the woody parts of the trees: it is possible that some of the loss might have been caused by leaching by rain (Kramer and Kozlowski, 1960). However, evidence for the role of foliar reserves to conifer shoot growth is largely indirect, but nonetheless convincing (Kozlowski, 1964). Results of sequential sampling strongly suggest that nitrogen and phosphorus and carbohydrates move from old to new shoots at bud break (Krueger, 1967). Isotope techniques will be needed to unequivocally demonstrate the export-import relationships.

Forrest (1969) estimated that only six per cent of the decrease in foliar phosphorus in old needles can be attributed to leaching. Therefore, for those nutrients showing a decrease in total content per leaf after initial development, the decrease must be attributed to internal redistribution within the tree for utilization at other actively growing centres. Obviously a change in the concentration of nitrogen in tissue may be brought about by a change in either the nitrogen or dry matter content of the tissue. Results need to be expressed on an absolute basis (i.e., per tree or per part) but this is often not possible when large mature trees are used.

In brief, the changes in needle dry weight and foliar N and P during the year are real and must be attributed to internal redistribution.

Seasonal variation of foliar nutrients in forest trees has been studied by a number of authors for a number of species. For example, Tamm (1951) with Betula spp., Puri and Gupta (1954) with Indian deciduous and evergreen species, Tam (1955) with Picea abies Karst and Pinus sylvestris L, Wells and Metz (1963) with Pinus taeda L, Miller (1966) with Pinus taeda L, Le Roy (1968) with Quercus pedunculata; and for Pinus radiata, Raupach (1967a) and Forrest (1969). In all these studies, little or no attention has been paid to the effect of tree vigour on the translocation of nutrients out of leaves in different parts of the crown.

In the present chapter, an account is presented of the effect of site on the translocation of N and P into and out of needles of different ages(1-4 years) in both the upper and lower crown of trees of the same age but of different vigour.

In foliar nutrient studies, it is useful to know how nutrient content varies with tree vigour and season. Admittedly, the percent patterns give no indication of translocation, but they help one interpret data obtained by sampling at a standard time during the year.

In summary, the aims of the study were (1) to examine the translocation patterns of foliar N and P in P. radiata and (2) to assess the relative seasonal variation of foliar N and P (in per cent) in trees of varying vigour.

5.2 MATERIALS AND METHODS

A 10-year-old tree was selected on each of three sites (Table 5.3). Two of the trees (Nos. 1 and 2) were growing on a yellow podzolic soil developed from undifferentiated granite at Pierce's Creek Forest while the third (Tree 3) was on a red podzolic soil developed from a shale parent material at Shannon's Flats, A.C.T. The differences between the two soils both morphologically and in water-holding capacity are striking (Appendix I). Trees 1 and 2 are within about 200 ft of each other; Tree 1 is of low vigour on an upper slope, while tree 2 is of much greater vigour on a lower slope. Tree 3 is located about four miles away at Shannon's Flats. All three trees are in stands of approximate 8 x 8 ft. spacing. However, because of poor survival on a low quality site, Tree 1 has probably been subjected to less within-stand competition than Trees 2 and 3. The latter trees are on the boundaries of well-stocked stands, i.e., they are shaded, at least in the lower half of the crown, from three sides. Also, Tree 3 on shale-derived soil has a particularly heavy branch and crown development. Climatic data for the study sites are summarised in Appendix I.

Table 5.3

Details of the three trees used in the study of seasonal variation in foliar N and P

	Tree 1	Tree 2	Tree 3
Tree age (years)	10	10	10
Total height (ft)	34.5	54.0	48.0
D.B.H. (in.)	7.78	9.40	8.90
Soil parent material	Undifferentiated granite		Shale
Soil type	Yellow podzolic		Red loam
Native vegetation	Dry sclerophyll forest		Wet sclerophyll
Slope (degrees)	15-20	20-25	20-25
Aspect	SE	N	SW
Position of tree	Well exposed to light	Shaded lower crown	Shaded lower crown
Nominal spacing (ft)	8 x 8	8 x 8	8 x 8

On each tree, seven branches were marked with plastic tape for permanent identification, six of the branches being on the north side of the tree and one on the south side. At regular intervals over a period of nearly 14 months, foliage was sampled at 13 locations on each tree (Fig. 5.1). These locations covered a range of branch and needle ages in both the upper and lower parts of the crown. Details of all the sample branches are summarised in Table 5.4.

At each sampling, 15-20 fascicles were sampled at random from each of the 13 locations. During the study period (September 1967 to November 1969) eleven separate samplings were taken at an average interval of 39 days.

Samples were taken to the laboratory and oven-dried, weighed and subsequently analysed for nitrogen and phosphorus using the standard procedure described in Appendix I. The fascicle weight was taken as the weight of the three needles excluding the fascicle sheath.

5.3 RESULTS AND DISCUSSION

The results are presented as seasonal patterns in:

(1) fascicle dry weight;
(2) total content of N and P per fascicle; and
(3) percentage content of N and P in the needles.

(1) and (2) deal with translocation whereas (3) deals with establishing a basis for the use of foliar nutrient content as obtained by sampling at a standard time during the year at a standard crown position.

5.3.1 Variation in fascicle dry weight

(a) Upper crown

Within the upper part of the crown, the weight of currently developing fascicles (locations 1 and 4) increased progressively through the year in each of the three trees. The 1-year fascicles on the uppermost branch (locations 2 and 5) decreased in weight from late September to November, i.e., as new growth was being

TABLE 5.4

Details of branches sampled for the study of seasonal variation in foliar N and P

Tree no.	Branch No.	Ht.above ground (ft)	Branch diam. (mm.)	Branch length (ft)	Aspect	Remarks
Tree 1	I	6.5	36	8.0	NNW	
	II	7.8	55	12.0	"	
	III	11.5	43	10.0	"	
	IV	17.2	30	7.0	W	
	V	18.8	21	2.5	WNW	
	VI	20.3	28	5.0	NNW	
	VII	20.3	28	4.0	SSE	
Tree 2	I	16.7	35	10.0	N	shaded
	II	18.4	30	7.0	NNW	shaded
	III	19.4	31	6.0	NNW	
	IV	28.0	26	6.0	"	
	V	30.7	28	6.0	"	
	VI	34.3	25	5.0	N	
	VII	34.3	29	7.0	SSE	shaded
Tree 3	I	10.0	30	7.0	NE	
	II	12.0	40	6.0	NE	
	III	14.0	50	10.0	N	
	IV	31.0	35	6.0	N	
	V	33.2	32	7.0	N	
	VI	35.5	27	5.0	N	shaded
	VII	35.5	27	5.0	S	shaded

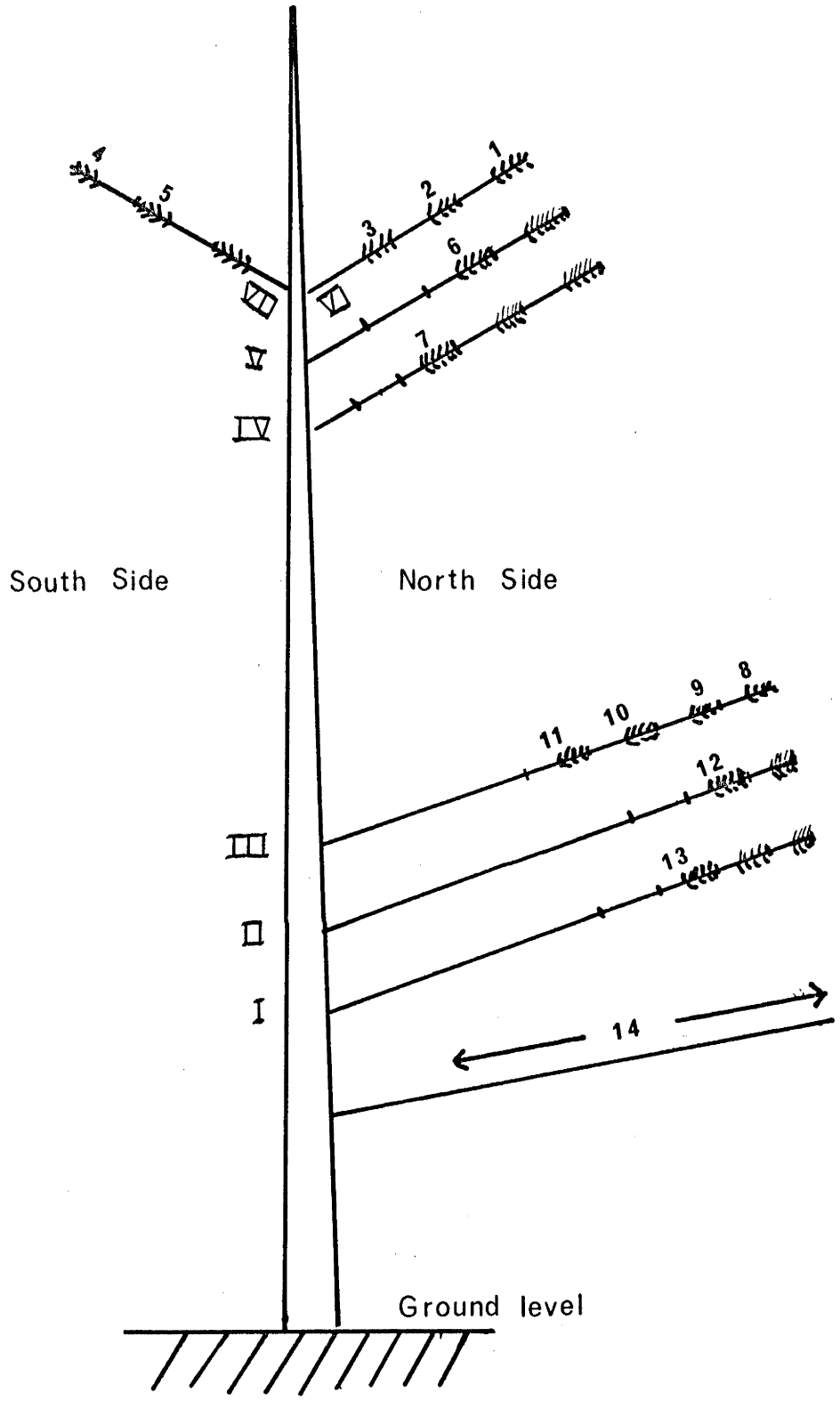


FIG 5.1 Diagram (not to scale) showing sampling positions (1-14) and sample branches (I-VII) within the crown of P. radiata for the seasonal study of foliar N and P.

initiated (Figs. 5.2 - 5.4). This weight decrease was least pronounced in Tree 1 (with low vigour on the granite-derived soil) and most pronounced in Tree 3) with high vigour on the shale-derived soil) where increase in weight did not begin until February or later. In this respect, the dry weight pattern of the tree on the shale-derived soil is distinctly different from those on the granite-derived soil.

Data for location 6 (1-yr needles on a 5-yr branch) and locations 3 and 7 (2-yr needles on 4 and 6-year branches respectively) are not complete for all 3 trees, but it is clear that seasonal variation in dry weight of these needles was not as pronounced as that in the 1-yr needles on the youngest branch.

The only tree to record a possible aspect effect was Tree 1 where needle weight on the north side (locations 1 and 2) was substantially greater than comparable weights on the south side in spite of similar branch vigour (Figure 5.2, Table 5.4).

(b) Lower crown

Within the lower crown (Figs 5.5 - 5.7) marked seasonal variation in fascicle dry weight was recorded only for Trees 2 and 3. Tree 1 (tree of low vigour on a granite-derived soil) generally exhibited a small decline in fascicle weight between September and December but thereafter rose slowly. In contrast, a decrease in needle weight was more evident in Tree 2, particularly for location 13 where increase in needle weight did not occur until after February. In Tree 3, seasonal variation in needle dry weight was extreme and substantial rises did not occur until April.

(c) Discussion

Differences between trees in the pattern of seasonal dry weight can be regarded as an index of the dynamic translocation of materials (carbohydrates and minerals) within the crown. In this respect, the translocation activity in the low-vigour Tree 1 was much less than that in the more vigorous trees. In the upper crown, translocation activity was greatest in the 1-year needles. Perhaps the more significant difference between trees

FIGS. 5.2 - 5.7

Seasonal patterns of fascicle dry weight for a number of positions (see Fig. 5.1) within the upper (Figs. 5.2 - 5.4) and lower (Figs. 5.5 - 5.7) crowns of P. radiata trees:

Tree 1: non-vigorous, on granite-derived soil.

Tree 2: vigorous, on granite-derived soil.

Tree 3: vigorous, on shale-derived soil.

FIG 5.2 Tree 1, upper crown

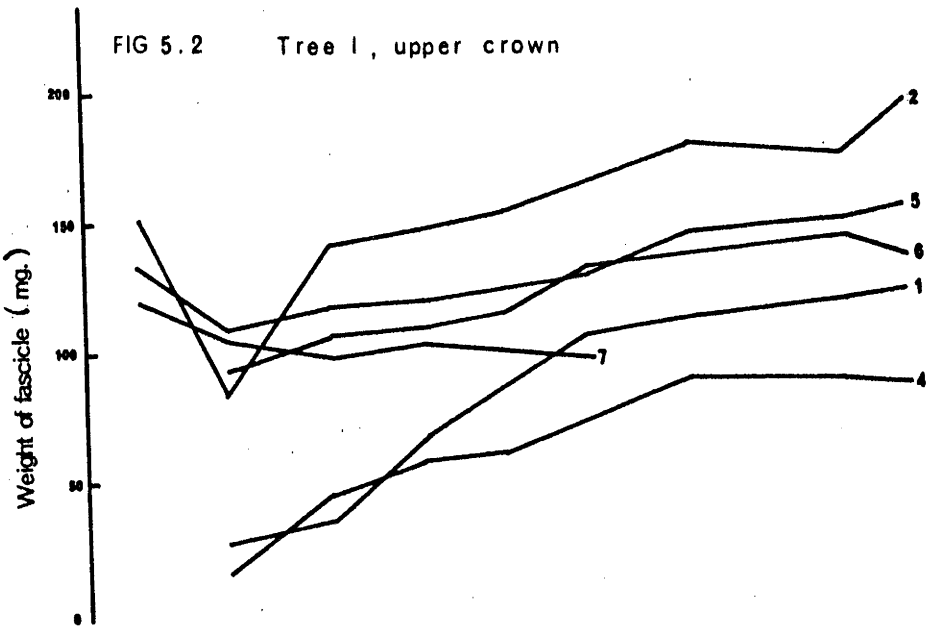
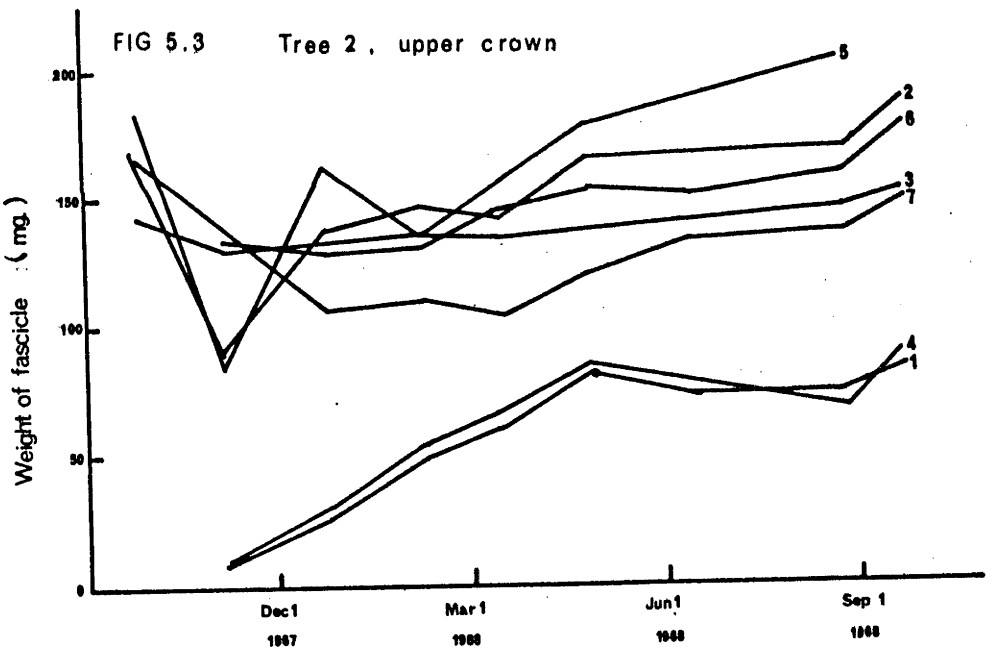


FIG 5.3 Tree 2, upper crown



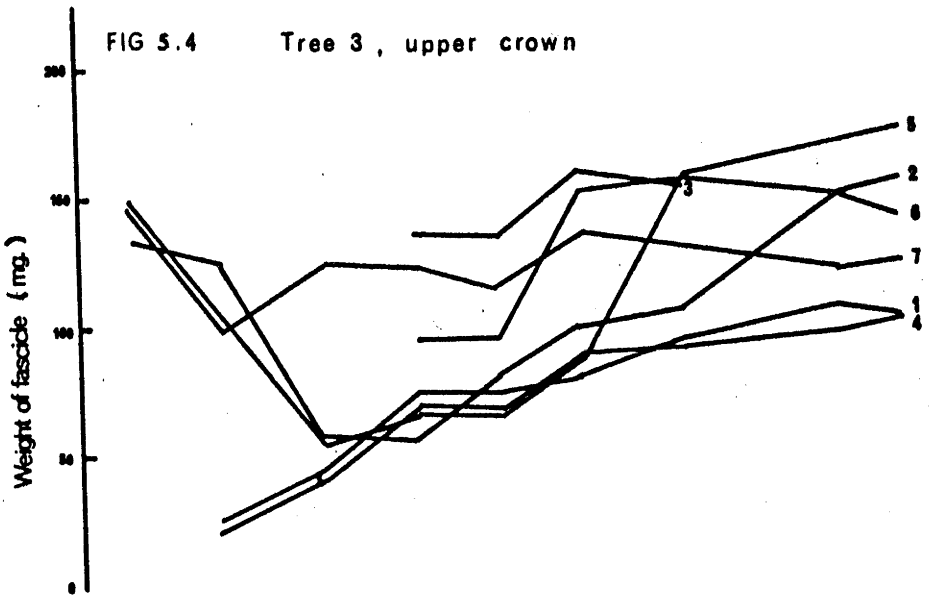


FIG 5.4 Tree 3 , upper crown

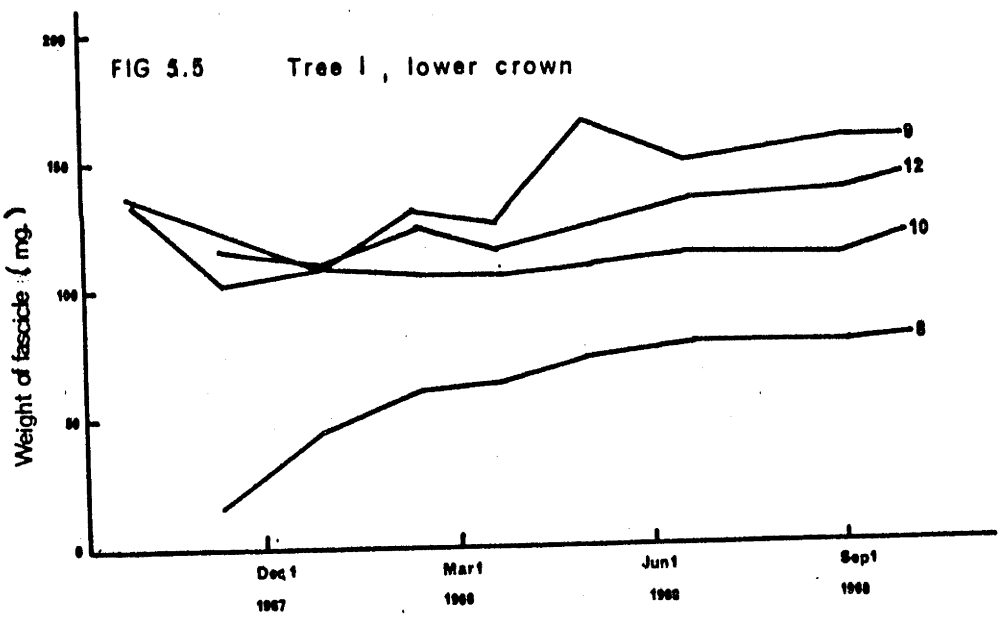


FIG 5.5 Tree 1 , lower crown

FIG 5.6 Tree 2 , lower crown

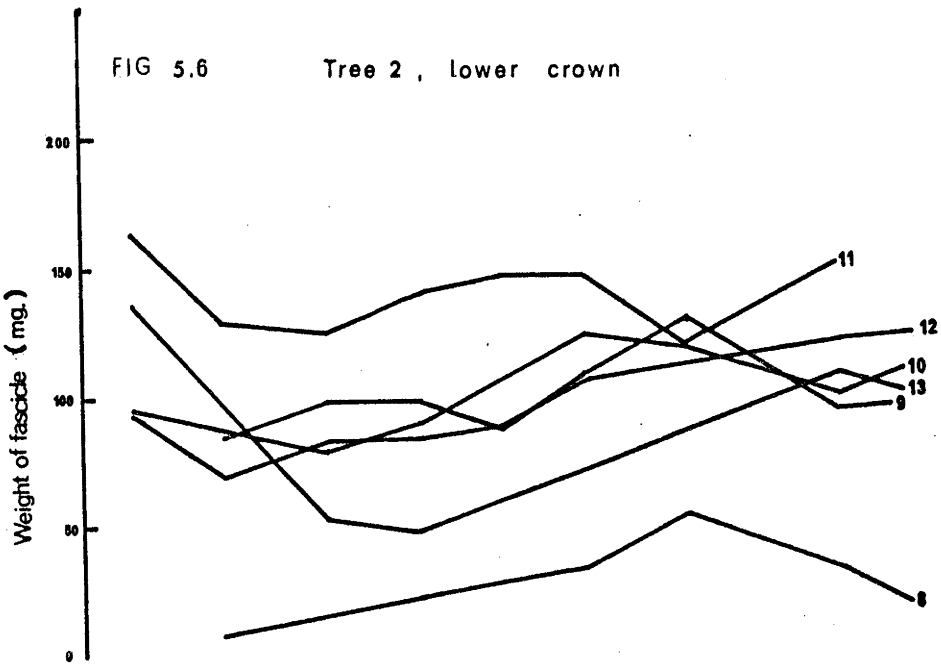
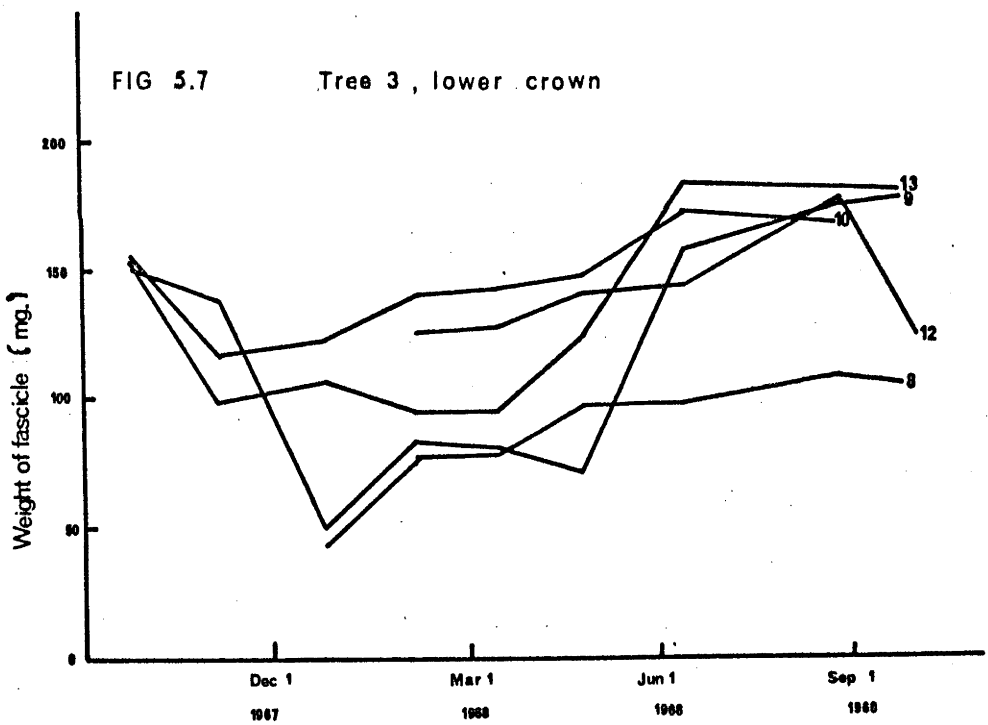


FIG 5.7 Tree 3 , lower crown



is that recorded in the lower crown. If the lower part of the crown can be regarded as a sink or pool for supply of nutrients or metabolic products to the expanding upper crown, then translocation from this sink or pool was far more active in the two high-vigour trees than in the low-vigour tree.

The patterns of dry weight variation in leaves can be related to growth patterns of the species. Pinus radiata has the potential for growing in height throughout the year. In southern Australia, the rate of growth tends to be at a minimum in late summer. It increases slowly in autumn and early winter, becomes progressively faster in late winter and early spring, and reaches its peak in mid or late spring: the growth rate then declines, the rate of decrease being much faster than the rate of increase in spring (Fielding, 1967a). This is essentially the pattern of withdrawal and build-up found in dry weight in old needles with, of course, local variations for each site e.g., an early growth initiation in spring or a delay in growth cessation in summer due to variation in temperature and soil moisture.

5.3.2 Total phosphorus content patterns

(a) Upper crown (Figs. 5.8-5.10)

For all trees, the increase in phosphorus content of developing needles (locations 1 and 4) was progressive throughout the year, but by August following their initiation, this content was still lower than that of older needles.

Phosphorus was withdrawn from older needles just before the spring, and this withdrawal continued through to summer before "recharging" began. A slow withdrawal of P from the needles of Tree 1 started as soon as the maximum was reached in June after a rise from the summer low (Fig.5.8). On the other hand, in Trees 2 and 3, a steady rise from the summer low did not reach a peak until September (Figs. 5.9-5.10).

(b) Lower crown (Figs. 5.11-5.13)

The patterns in all trees in the lower crown were similar with a summer low and a steady rise of foliar P until September.

FIGS. 5.8 - 5.13

Seasonal patterns of total phosphorus in needles for a number of positions (see Fig. 5.1) within the upper (Figs. 5.8 - 5.10) and lower (Figs. 5.11 - 5.13) crowns of P. radiata trees:

Tree 11 : non-vigorous, on granite-derived soil.

Tree 2 : vigorous, on granite-derived soil.

Tree 3 : vigorous, on shale-derived soil.

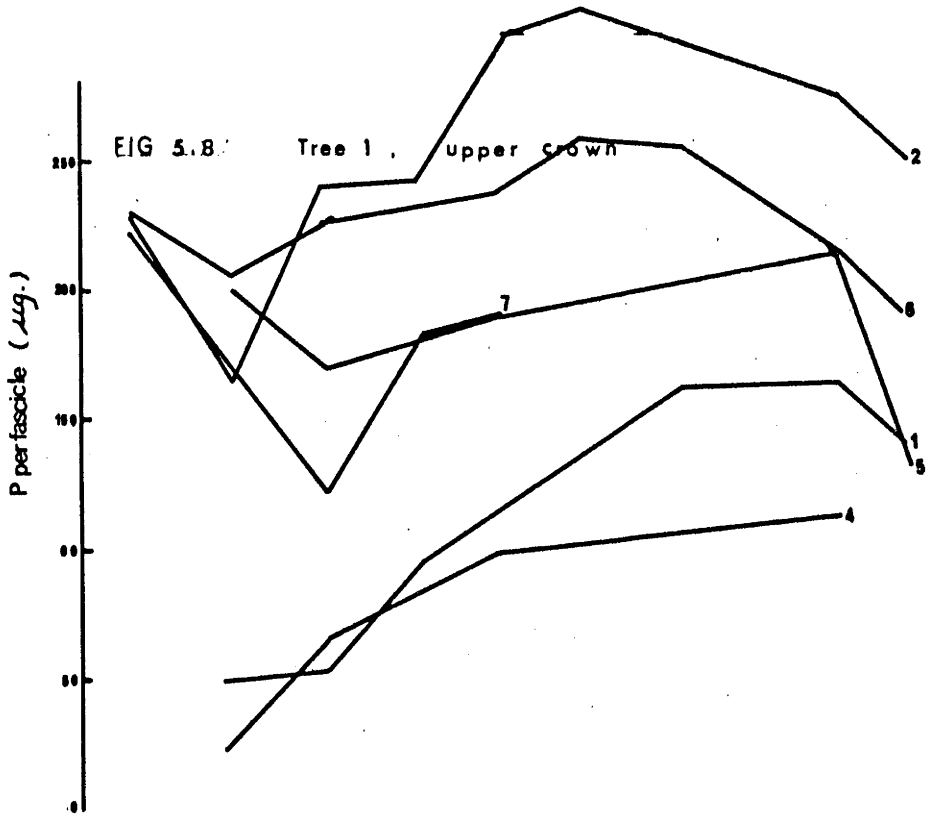


FIG 5.8 Tree 1 , upper crown
P per fascicle (µg.)
250
200
150
100
50
0
2
6
7
1
5
4

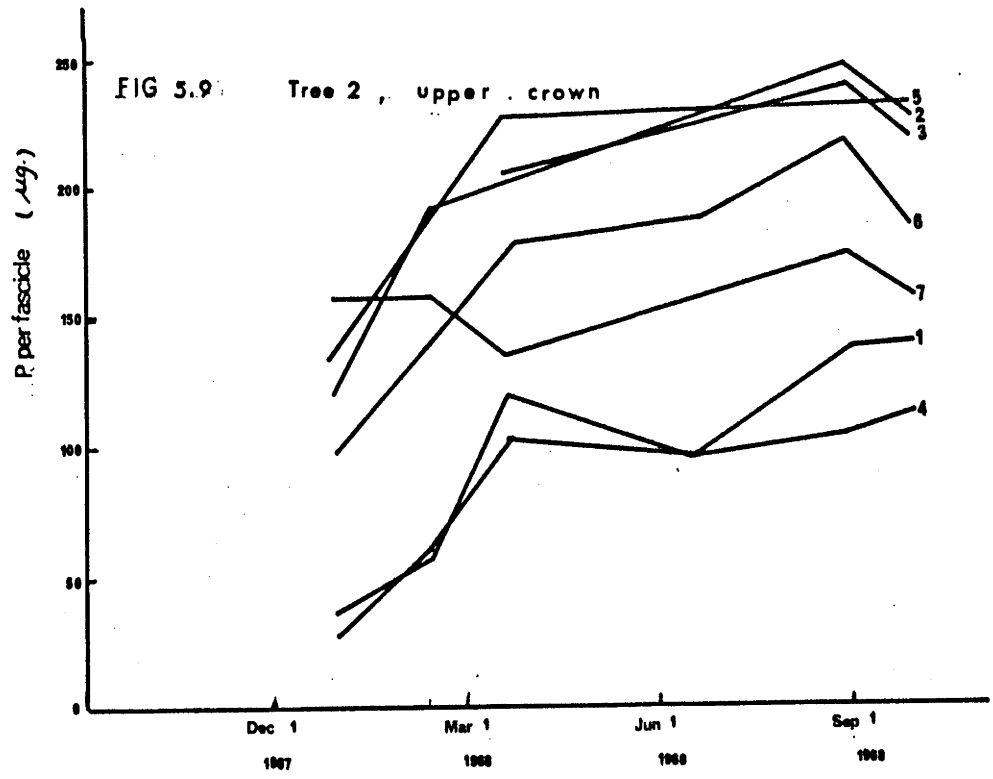


FIG 5.9 Tree 2 , upper . crown
P per fascicle (µg.)
250
200
150
100
50
0
5
2
3
6
7
1
4
Dec 1
1987
Mar 1
1988
Jun 1
1988
Sep 1
1988

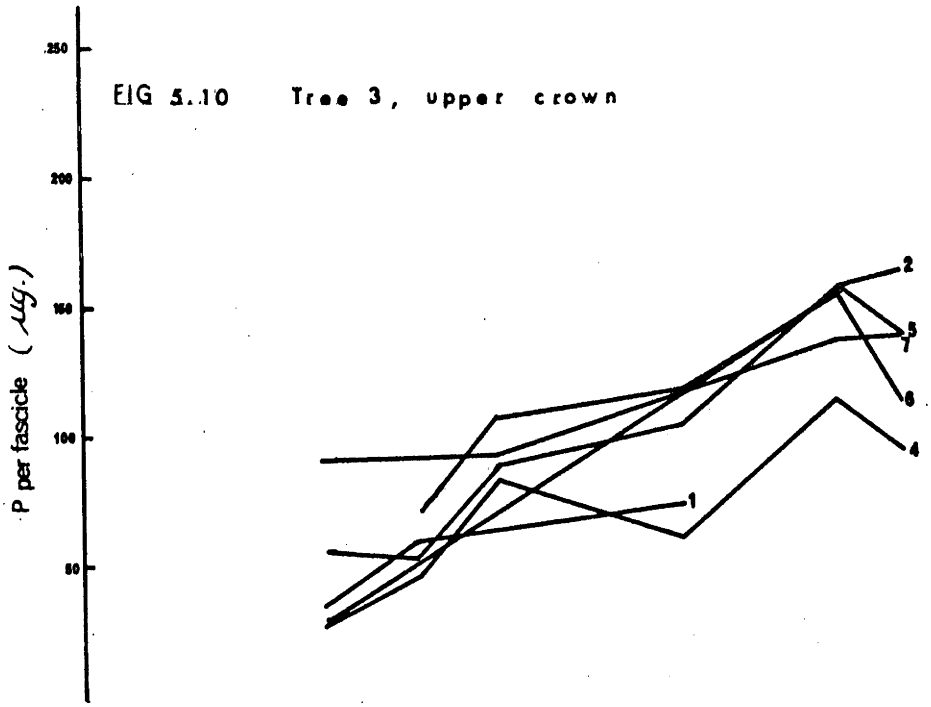


FIG 5.10 Tree 3, upper crown

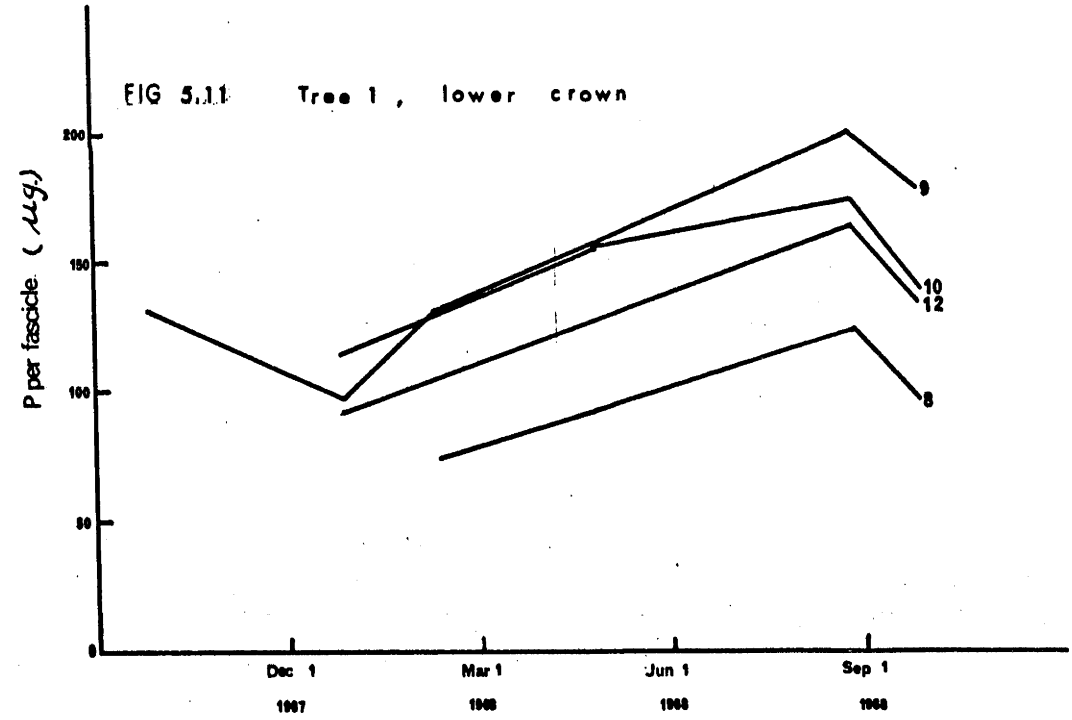


FIG 5.11 Tree 1, lower crown

FIG 5.12 Tree 2 , lower crown

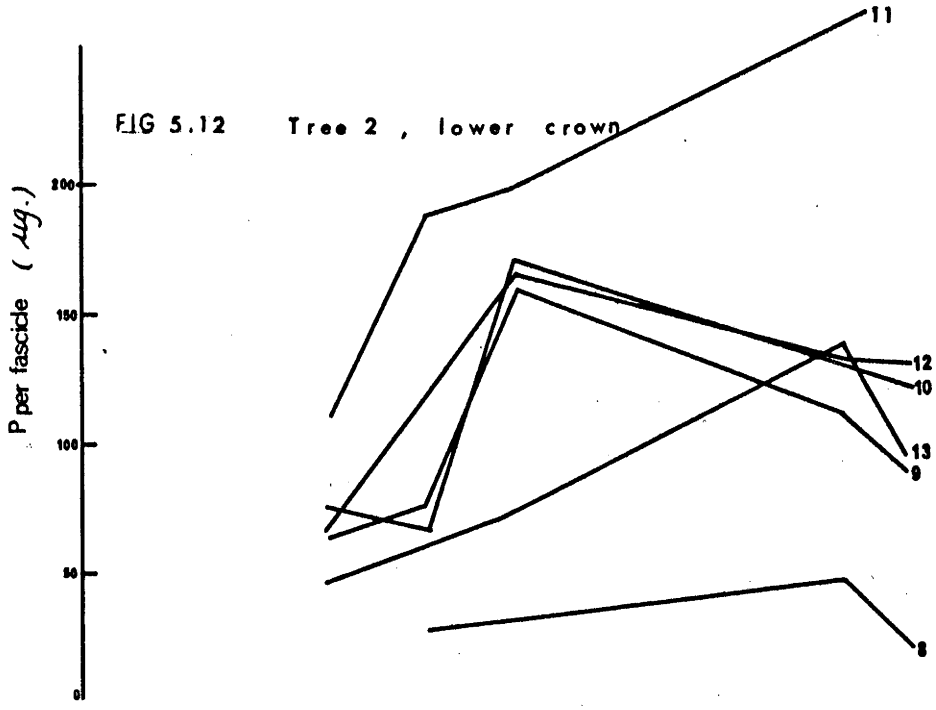
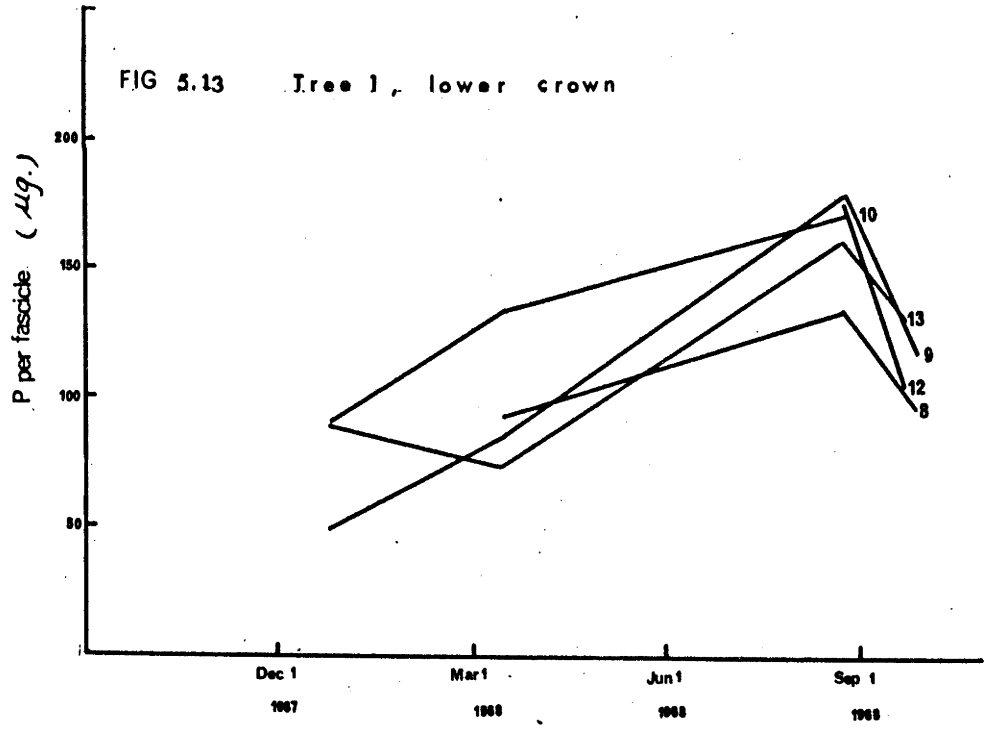


FIG 5.13 Tree 1 , lower crown



Again the difference in total P between several locations is less in the shale-soil tree than in the granite-soil trees.

(c) Discussion

Examination of the translocation patterns of P in three trees of varying vigour reveals certain differences. In the upper crown, the low-vigour Tree 1 is withdrawing P from the needles for a much longer period of the year than the more vigorous trees. This may mean that the tree has to use almost continuously the limited amount of P it has got. The P status of the three trees at July 15, as interpolated from the graphs, was as follows:

Tree 1	0.17 per cent
Tree 2	0.14 " "
Tree 3	0.10 " "

Consequently Tree 1 has a relatively high P status, and if these percentages are accepted for use, an explanation must be sought elsewhere.

In the lower crown of Tree 1, the seasonal pattern is different from that in the upper crown, the withdrawal period being much shorter. This indicates that P in the upper crown is used before that in the lower crown. In other words, the translocation is better in the upper crown in this tree. And because of the non-synchronisation of translocation between crown parts, one might infer that translocation of P from the lower crown to the upper crown is inefficient.

In Trees 2 and 3, the more vigorous trees, the seasonal pattern is the same for both parts of the crown, and the withdrawal period is short. This suggests that, because of the synchronisation between crown parts in translocation, the translocation from the lower crown to the upper crown is efficient. Consequently, although they have a low P status (0.14 and 0.10 per cent respectively) Trees 2 and 3 do not have to draw on the old needles for a long period during the year to maintain growth.

5.3.3 Total nitrogen content patterns

(a) Upper crown (Figs. 5.14-5.16)

As for P, N was withdrawn from the needles of Tree 1 for a longer period of the year than from those of Trees 2 and 3 (Figs. 5.15-5.16), and in contrast to Trees 2 and 3, the N withdrawal in Tree 1 was not as pronounced and the trend not as regular or definite as that for P.

(b) Lower crown (Figs. 5.17-5.19)

Within the lower crown, N content in Tree 1 (Fig. 5.17) was more or less stable for the summer-autumn period. It then increased to a maximum at the end of winter. This comparatively stable period of low N content was, however, not clear in Tree 2 (Fig. 5.18) and definitely lacking in Tree 3 (Fig. 5.19). And again, the N pattern in Tree 1 was also different to the P pattern in the same tree (Fig. 5.11).

In Tree 1, the seasonal pattern of N content in the lower crown was again different from that in the upper crown. This is similar to P patterns in the same tree. However, it is not the case with Trees 2 and 3 which show a steady rise of total N content from the summer low to September peak in both crown parts (the data in Fig. 5.19 are inadequate, and the use of data for locations 10 and 12 is doubtful).

(c) Discussion

Firstly, as in the case for P, the translocation pattern of N in the lower crown was different from that in the upper crown in the low-vigour Tree 1, but not in the more vigorous trees.

Secondly, the irregular and not very pronounced pattern of N in the upper crown, and a stable prolonged summer low in the lower crown, may indicate a somewhat sluggish translocation of N compared with that of P. For example, the stable and prolonged summer low may mean a delay in the build-up of N in the needles due to either lack of N and/or inadequate translocation in the summer-autumn period. Indeed, the N status of Tree 1 was 1.20 per cent compared with 1.60 and 1.70 per cent for Trees 2 and 3

FIGS. 5.14 - 5.19

Seasonal patterns of total nitrogen in needles for a number of positions (see Fig. 5.1) within the upper (Figs. 5.14 - 5.16) and lower (Figs. 5.17 - 5.19) crowns of P. radiata trees:

Tree 1: non-vigorous, on granite-derived soil.
Tree 2: vigorous, on granite-derived soil.
Tree 3: vigorous, on shale-derived soil.

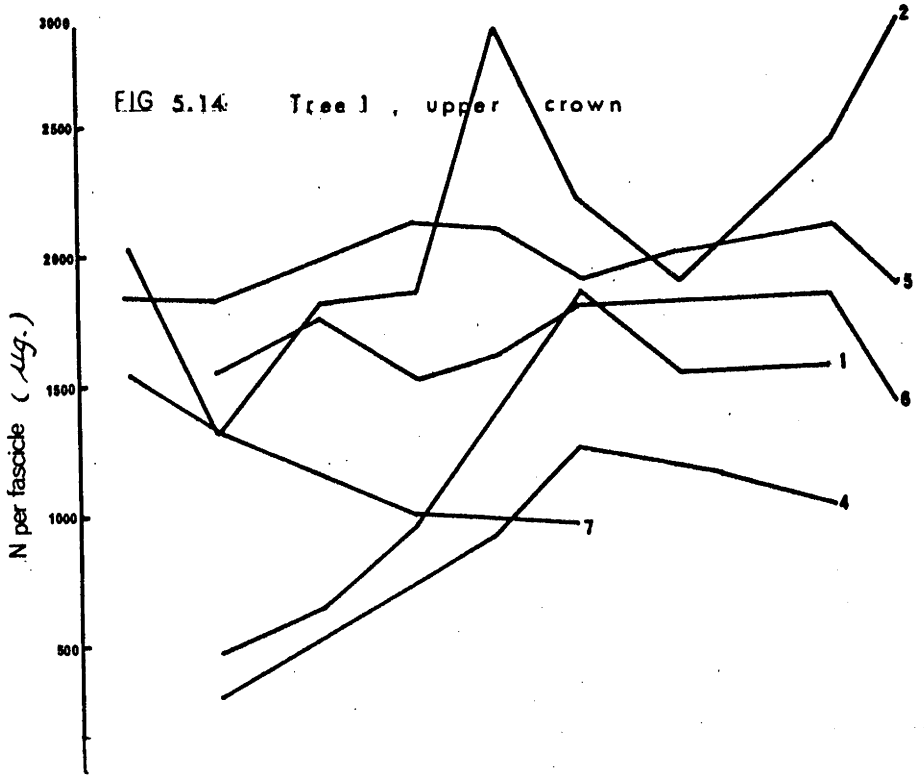


FIG 5.14 Tree 1 , upper crown

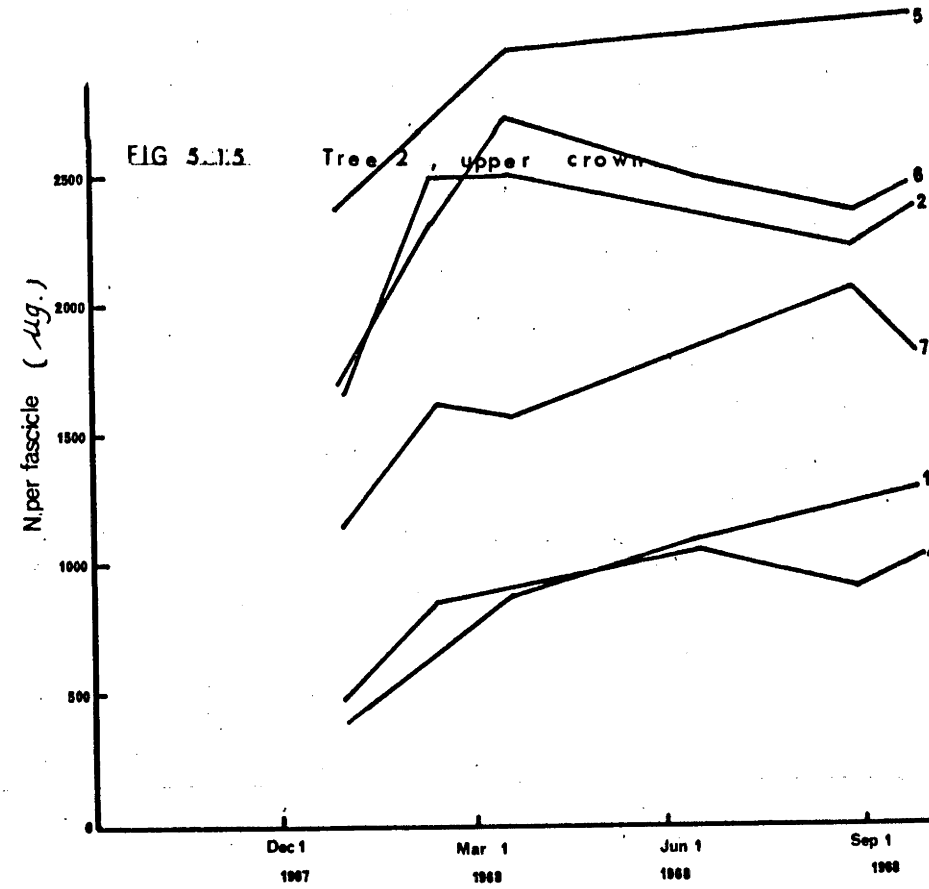


FIG 5.15 Tree 2 , upper crown

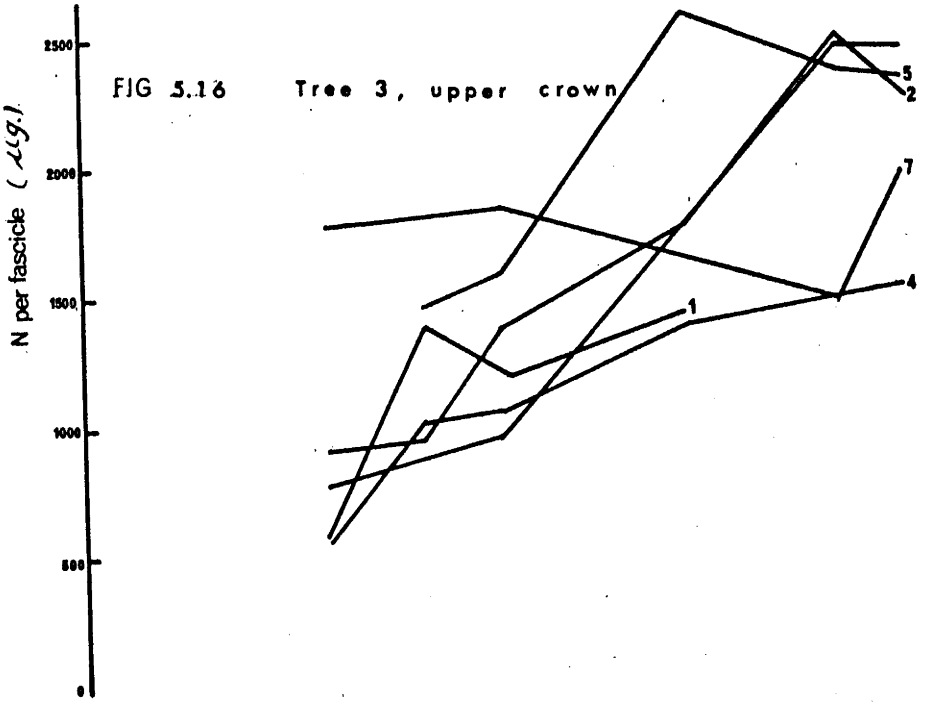


FIG 5.16 Tree 3, upper crown

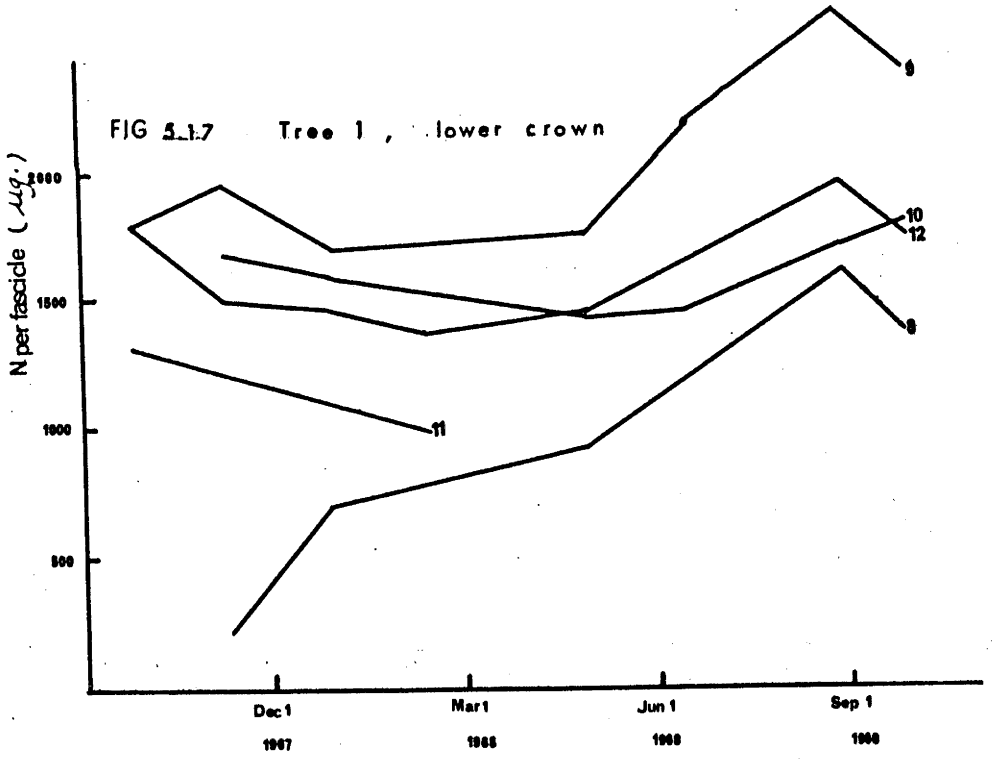


FIG 5.17 Tree 1, lower crown

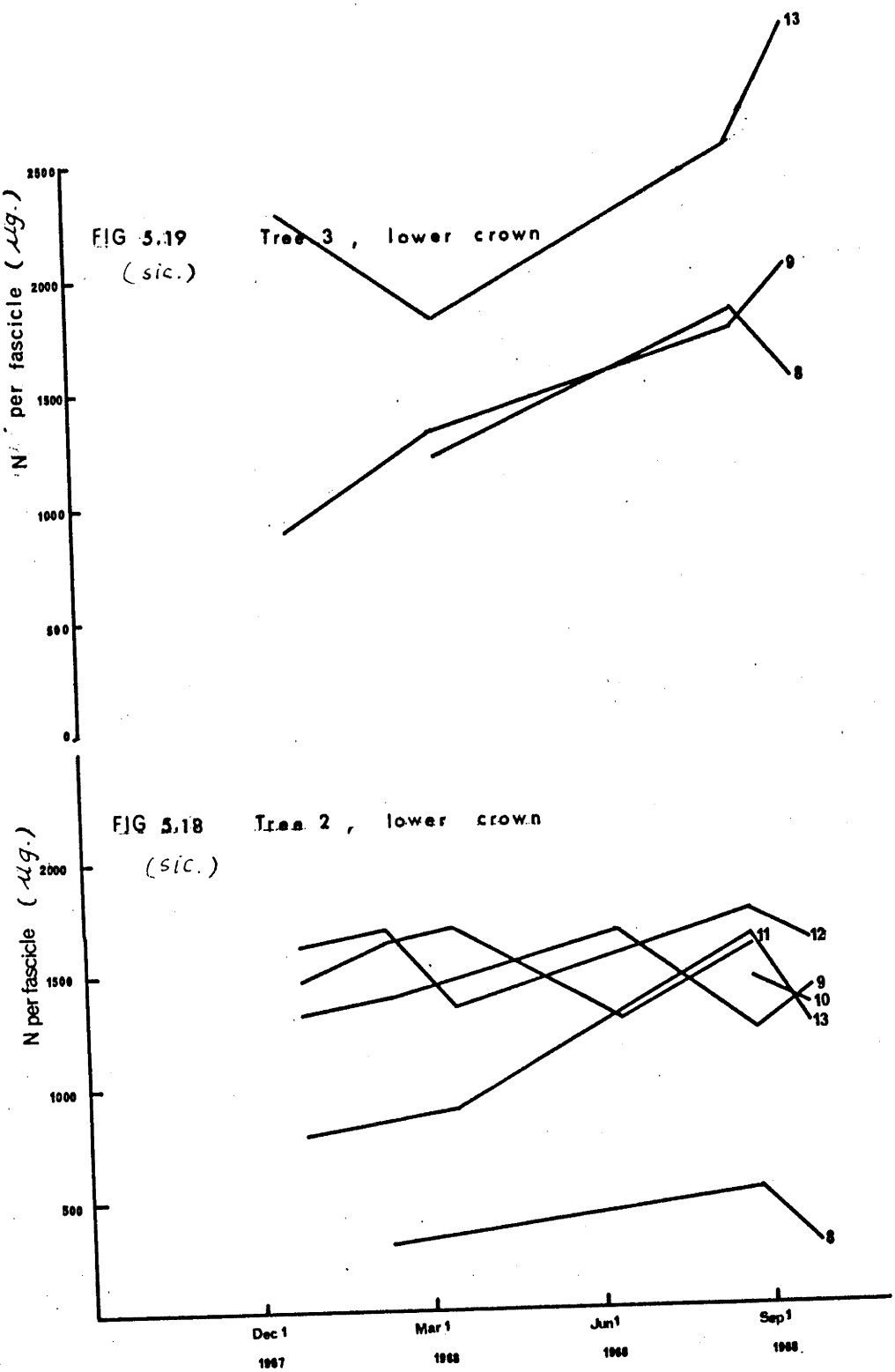


FIG 5.19 Tree 3, lower crown (sic.)

FIG 5.18 Tree 2, lower crown (sic.)

respectively (July estimate at location 2). Undoubtedly, the moisture supply is not adequate for Tree 1 during summer.

5.3.4 Discussion of translocation patterns

The seasonal variation in foliar dry weight and nutrient content in P.radiata trees of varying vigour could be summarised as follows: (1) There is some evidence that, in a low-vigour tree, the translocation of both N and P from the lower to the upper crown is more restricted than in more vigorous trees. (2) The N translocation in a low-vigour tree is more irregular and has a less consistent trend than that of P, especially in the lower crown. This suggests P may be better translocated than N in a low-vigour tree.

The differential patterns of N and P translocation may be related to the inherent mobility of the two elements: N being of lower mobility. For example, Leyton (1958) was able to correlate the annual height growth of a number of conifers with the P status of current-year needles; on the other hand, current-year growth was governed by the N reserves of the previous year, presumably due to the lower mobility of N. In this study, the differential mobility was only found in the low-vigour tree. Furthermore, the vertical and horizontal gradients in nutrient concentration examined in previous chapters cannot be explained in terms of greater mobility of P or slower mobility of N. For example, in Chapter 3, there was no vertical gradient for P in any of the plots of varying vigour examined, but there was a gradient for N in the two more vigorous plots. There was no horizontal gradient in any plot for either N or P.

In Chapter 4, with four stands in an age series on a low-quality site, the only vertical gradient recorded was for P in the youngest stand. There was no significant vertical gradient in any stand on this low-quality site.

In conclusion, if a slower mobility of N than P is accepted, the differential mobility is likely to show up in low-vigour trees on a low-quality site and not in vigorous trees on a high-quality site.

Clearly further research is needed to relate the sluggish translocation of N to specific site factors, for example, moisture supply, which is undoubtedly different for low and high quality sites.

The sluggish translocation of N may be related to the relative foliar levels of the nutrients themselves; however, this seems unlikely because the low-vigour Tree 1 has a N status of 1.20 per cent and a P status of 0.170 per cent, that is, a foliar N:P ratio of 7.0. This is well within the range of 5-16 associated with good growth for the species. This point will be discussed further after examining the seasonal patterns of foliar N and P content.

5.3.5 Seasonal variation in foliar phosphorus content

As mentioned before, the seasonal variation in foliar nutrient content would not give any indication of nutrient translocation. For example, an increase in P per cent would not necessarily mean that additional P had been moved into the needles; rather the increase could result from a movement of carbohydrates out of the needles. Nevertheless, to understand the meaning of foliar nutrient content, it is necessary to study its variation with season, tree vigour, and other environmental factors.

(a) Upper crown (Figs. 5.20-5.22)

The first striking feature of the P content is the relatively low value for Tree 3 (Fig. 5.22). This is in direct contrast to the relative content of nitrogen in the foliage of the three trees. As shown earlier, the highest P concentration was in the low-vigour tree.

In the low-vigour Tree 1, P per cent ranged between 0.150 and 0.200 for all locations from spring through to the following winter before falling away to a clearly defined low (0.100-0.125 per cent) in August-September. The fluctuation in foliar-P was more or less parallel for all sampling locations, and while younger needles on the uppermost branch (locations 2 and 5) had generally the higher foliar P values, differences between these

and other needles were not pronounced (Fig. 5.20).

The fluctuation of foliar P per cent in Tree 2 was greater than in Tree 1, particularly in the newly developing needles (locations 1 and 4) (Fig. 5.21). One and 2-yr needles (locations 2, 5, 6, 7) were at a clearly defined low point in summer but built up by early autumn, remaining stable through winter, until P per cent fell again at the beginning of spring. The pattern of fluctuation in foliar P was just as strong in Tree 3 (Fig. 5.22): a summer low-early autumn peak - winter low - early spring peak - spring low pattern was characteristic of most locations.

(b) Lower crown (Figs. 5.23-5.25)

Of the three trees, the most vigorous tree was Tree 2. This tree had the greatest degree of fluctuation of foliar P per cent in the lower crown and a considerable fluctuation in the upper crown (Fig. 5.24).

In relation to its vigour, Tree 3 had a very low foliar P level (0.100 per cent). Fluctuation in the foliar P level was very pronounced in the upper crown, but was stable at a relatively low level in the lower crown (Fig. 5.25).

(c) Discussion

In the low-vigour tree with high-foliar P concentration (Tree 1), there was less seasonal fluctuation in P concentration than in other trees, both in the upper and lower crown. In a more vigorous but lower-P status tree, seasonal fluctuation in P concentration was stronger and was particularly apparent in older needles of the lower crown.

5.3.6 Seasonal variation in foliar nitrogen content

(a) Upper crown (Figs. 5.26-5.28)

The N status of the three trees at July 15, as interpolated from the graphs, was as follows :

Tree 1	1.20 per cent N
Tree 2	1.60 per cent N
Tree 3	1.70 per cent N

FIGS. 5.20 - 5.25

Seasonal patterns of phosphorus percent in needles for a number of positions (see Fig. 5.1) within the upper (Figs. 5.20 - 5.22) and lower (Figs. 5.23 - 5.25) crowns of P. radiata trees:

Tree 1: non-vigorous, on granite-derived soil.
Tree 2: vigorous, on granite-derived soil.
Tree 3: vigorous, on shale-derived soil.

FIG 5.20 Tree 1, upper crown

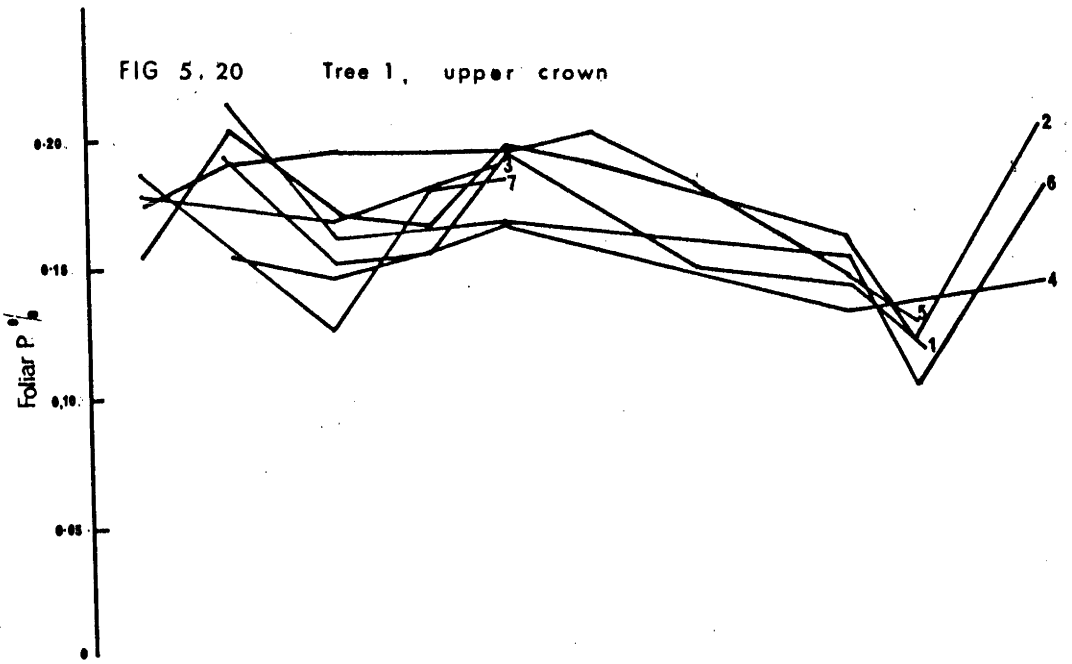


FIG 5.21 Tree 2, upper crown

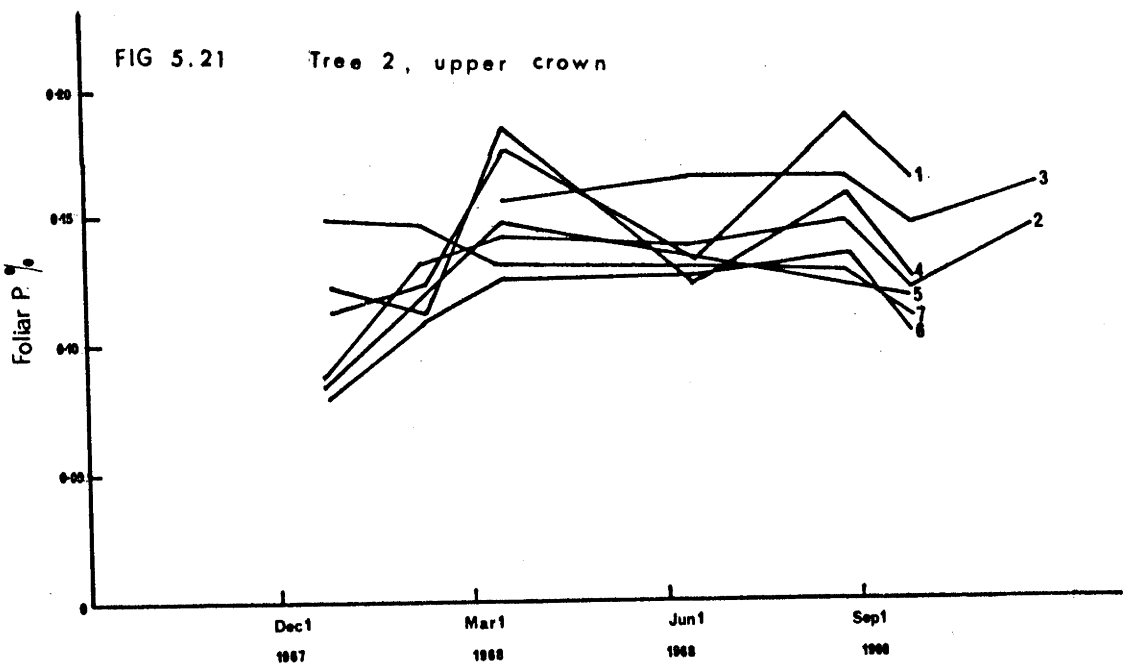


FIG 5.24 Tree 2 , lower crown

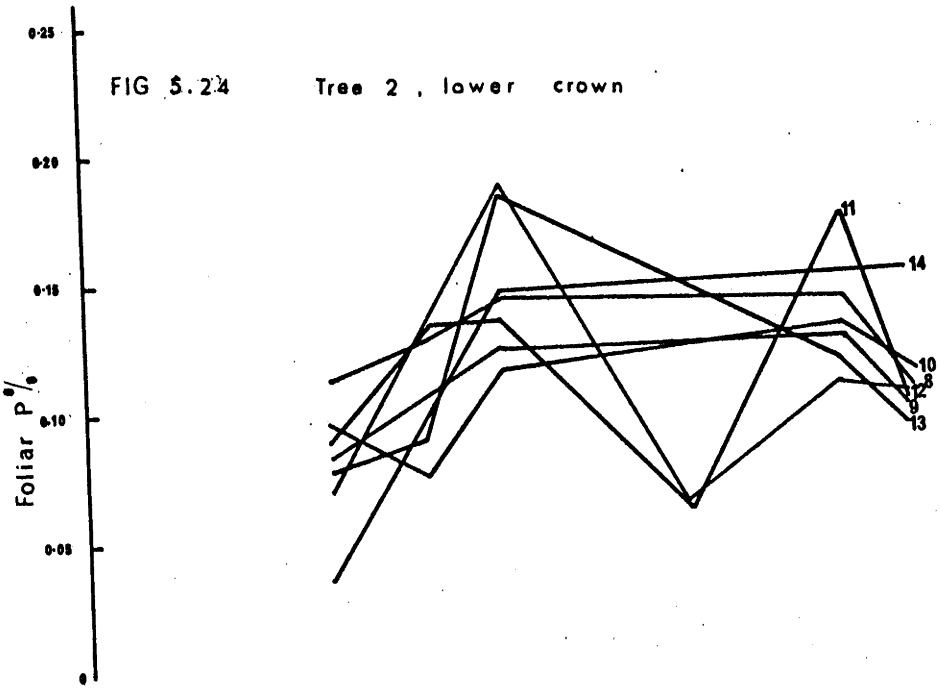
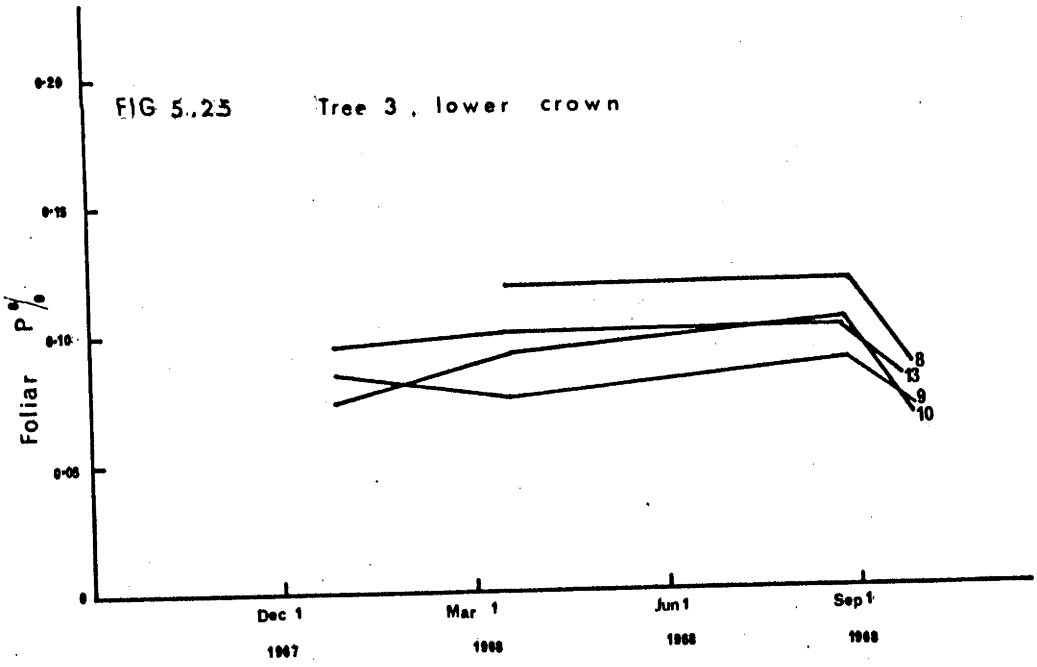


FIG 5.25 Tree 3 , lower crown



This large difference between Tree 1 and Trees 2 and 3, however, is not reflected in the N per cent level over the year as a whole. Outside the period May-September, N per cent in Tree 1 ranged from around 1.50 per cent to as high as 1.80. Most recordings for Trees 2 and 3 also fell within this range. Moreover, the fluctuation in foliar N content in Tree 1 (Fig. 5.26) was greater than that of Tree 2 (Fig. 5.27) and particularly of Tree 3 (Fig. 5.28). In Tree 1, for example, N content was at a peak about November and then declined irregularly at all locations until the following September; in Tree 3, the N content showed only slight seasonal variation and a more restricted range of variation within the crown.

(b) Lower crown (Figs. 5.29-5.31)

Within the lower crown, the pattern of variation in N content is quite different; here N per cent at all locations in the vigorous Tree 3 dropped sharply from December through August. In contrast, the low-vigour, low-N status Tree 1 had a fairly stable N per cent throughout the year rising through winter, before declining again in the spring flush. Tree 2 is intermediate between Tree 1 and 3 in that it shows a general but slow decline in N per cent throughout the summer/winter period (Fig. 5.30).

(c) Discussion

The very high N content tree, Tree 3, on shale has a small range of foliar N at different locations within the upper crown. There was a very sharp seasonal fluctuation in the lower crown. The low-vigour Tree 1 has the widest range of foliar N at different locations in both upper and lower crowns, and a greater degree of foliar N fluctuation in the upper crown than in the high N tree. The tree of intermediate N content, Tree 2, which is the most vigorous tree, is also intermediate between Trees 1 and 3 in the range of N per cent at different locations and the extent of fluctuation in foliar N at the one sampling position. The most marked difference between the trees lies in the smaller fluctuation in N per cent in the high N trees throughout the year.

FIGS. 5.26 - 5.31

Seasonal patterns of nitrogen percent in needles for a number of positions (see Fig. 5.1) within the upper (Figs. 5.26 - 5.28) and lower (Figs. 5.29 - 5.31) crowns of P. radiata trees:

Tree 1: non-vigorous, on granite-derived soil.
Tree 2: vigorous, on granite-derived soil.
Tree 3: vigorous, on shale-derived soil.

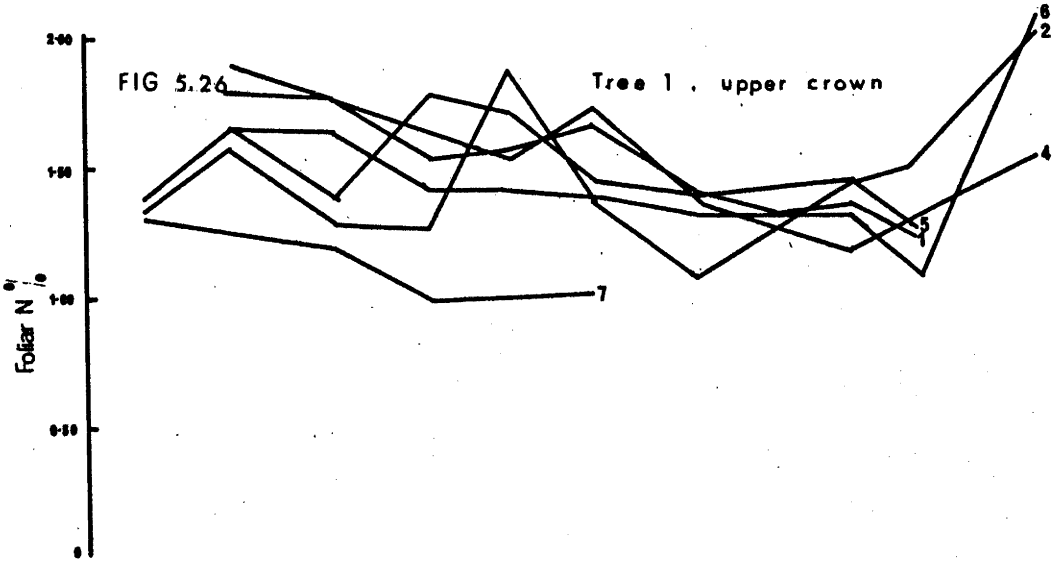


FIG 5.26
Tree 1 , upper crown
Foliar N %
2·00
1·50
1·00
0·50
0
6
2
4
5
7

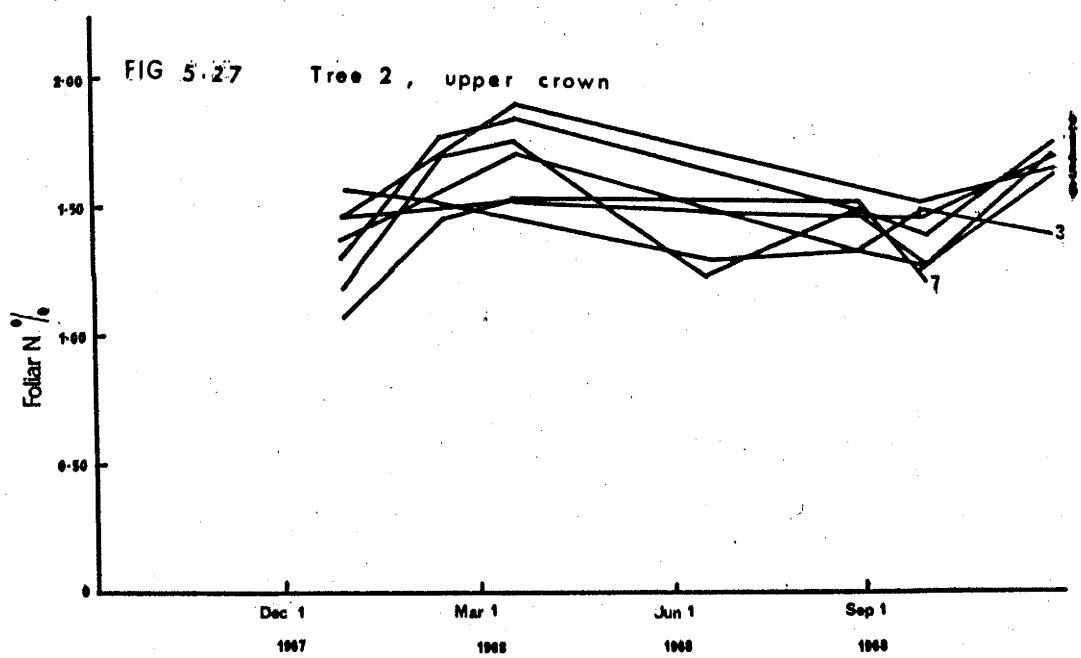


FIG 5.27
Tree 2 , upper crown
Foliar N %
2·00
1·50
1·00
0·50
0
3
7
Dec 1
1967
Mar 1
1968
Jun 1
1968
Sep 1
1968

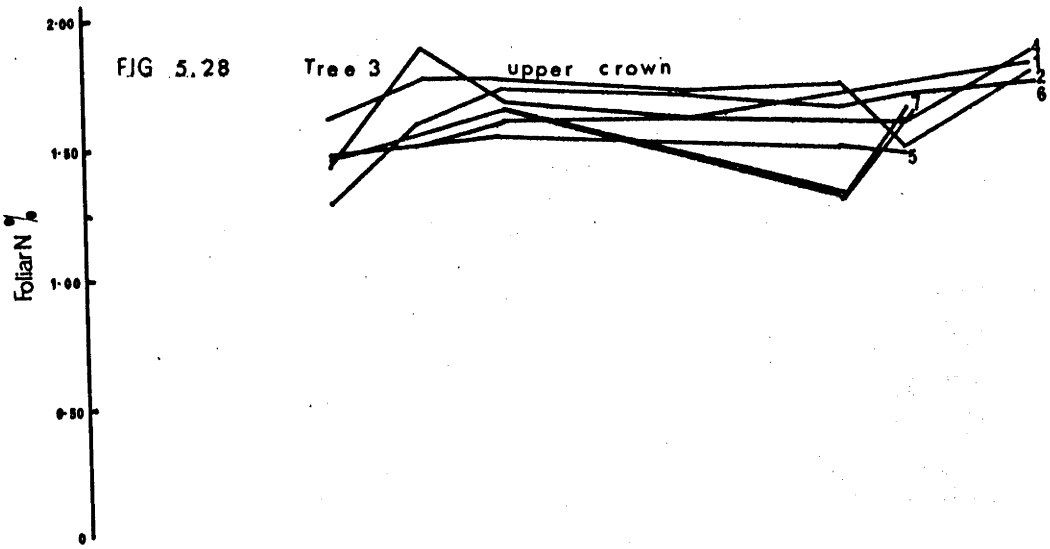


FIG 5.28
Tree 3
upper crown
Foliar N %
2·00
1·50
1·00
0·50
0
1
2
3
4
5
6
7

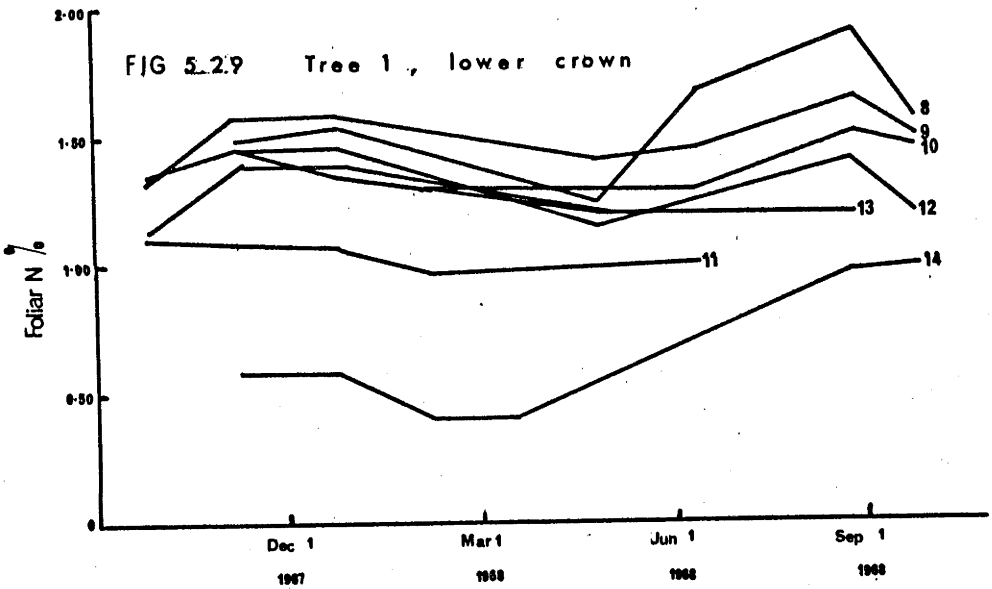


FIG 5.29
Tree 1 , lower crown
Foliar N %
2·00
1·50
1·00
0·50
0
8
9
10
11
12
13
14
Dec 1
1967
Mar 1
1968
Jun 1
1968
Sep 1
1968

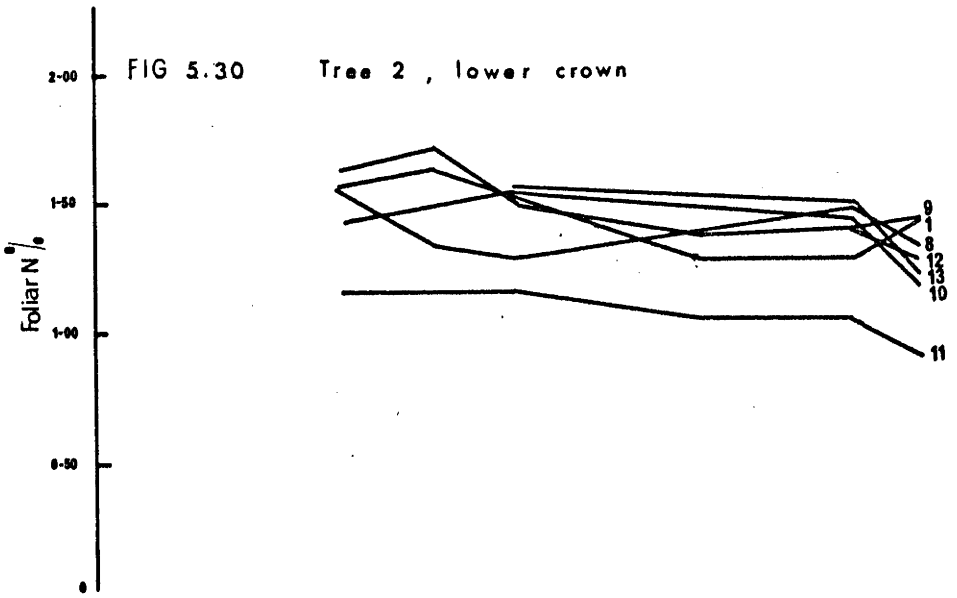


FIG 5.30
Tree 2 , lower crown
Foliar N %
2·00
1·50
1·00
0·50
0
9
1
8
12
13
10
11

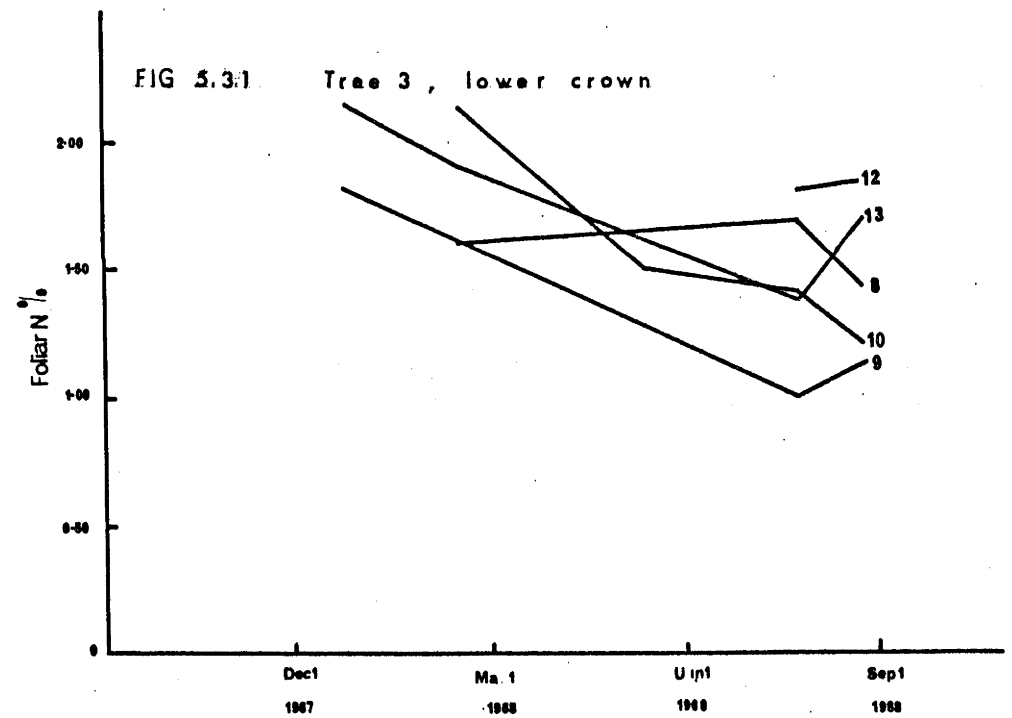


FIG 5.31
Tree 3 , lower crown
Foliar N %
2·00
1·50
1·00
0·50
0
12
13
8
10
9
Dec1
1967
Ma. 1
1968
U in1
1968
Sep1
1968

5.3.7 Discussion of seasonal variation in foliar nutrient content

What do the patterns of N and P per cent reveal? In earlier chapters, differences between trees on different sites, in the horizontal and vertical N and P gradients were recorded, and it seemed that these could be related to tree vigour. Data on N and P content from the present study do not present any clear indication of whether this is so. Taking the N and P per cent range respectively, for upper and lower crowns over the year, the following pattern emerges:

Table 5.5

Seasonal range of foliar nutrient content in upper and lower crowns of trees of varying vigour

	Upper crown	Lower crown
Phosphorus		
Tree 1 (Low vig.)	0.20-0.15	0.14-0.09
Tree 2 (High vig.)	0.16-0.10	0.15-0.08
Tree 3 (High vig.)	0.12-0.07	0.12-0.07
Nitrogen		
Tree 1 (Low vig.)	1.8-1.1	1.7-1.1
Tree 2 (High vig.)	1.8-1.2	1.6-1.2
Tree 3 (High vig.)	1.7-1.3	1.7-1.2

For P per cent, the range is lower in the lower crown than in the upper crown only for Tree 1. For N per cent, the range is similar for all three trees in the upper crown, and only slightly lower in the lower crown. There is no clear indication that the vertical gradient is related in any direct way to tree vigour. The striking feature of the N and P per cent data is the large seasonal fluctuation at any sampling position. The patterns are not necessarily similar from tree to tree. Thus, a sampling at a given time of the year could produce a misleading picture of nutrient status. For example, the N per cent of the

three trees at a winter sampling of 1-year needles in the upper crown showed very wide differences in N per cent. However, taken over the year as a whole, the N per cent range for all upper crown needles sampled was much the same for each of the three trees.

Where only foliar nutrient per cent data are used to interpret nutritional status, the way the foliar P per cent fluctuates throughout the whole year (range, degree of fluctuation, and times of fluctuation) would give a more reliable picture of the trees' use of P than would any single standard sampling. Where P is expected to be used efficiently, as in vigorous trees, large fluctuations would be expected at different positions in the crown; where P is not being translocated efficiently as in low-vigour trees, fluctuations in P per cent may be smaller.

The relationship between tree vigour and foliar N per cent may be different from that between vigour and foliar P per cent. In the more vigorous Trees 2 and 3, the N per cent pattern was relatively stable throughout the year in the upper crown. By contrast, in the low-vigour Tree 1, the N per cent pattern fluctuated more (although broadly similar). In the lower crown, the N per cent patterns were relatively stable in both the low and high-vigour Trees 1 and 2. Therefore, the N per cent patterns do not express vigour differences as well as the P patterns.

Having established a relationship between seasonal fluctuation in nutrient content and tree vigour, it is interesting to see how the foliar N:P ratio varies with tree vigour throughout the year.

In Table 5.6, the ratio has been calculated for the three trees, for both upper and lower crowns, using the current needles (locations 1, 4 and 8 in Fig. 5.1).

Table 5.6

N:P ratios in the needles of P.radiata trees of varying vigour through the year

Tree Vigour	Parent-rock	Crown position	Spring	Summer	Autumn	Winter
Low	Granite	Upper	10.6	11.0	10.0	10.8
		Lower	14.0	13.0	10.0	12.9
High	Granite	Upper	11.5	12.8	8.8	9.7
		Lower	14.9	11.7	9.3	10.0
High	Shale	Upper	20.7	16.0	18.4	18.9
		Lower	12.7	13.7	13.5	13.9

There are two striking features in Table 5.6:

(1) The low-vigour tree had ratios (10.0-14.0) well within the optimum range (5-16) associated with good growth (Raupach, 1967a); while in the more vigorous trees, the ratios ranged from 8.8-14.9 and 12.7-20.7 respectively. Thus, the use of an optimum ratio of 10 as suggested by Raupach could be misleading.

(2) On the other hand, if the seasonal range of the N:P ratio is used, a more reliable picture emerges: the most vigorous tree (Tree 2) had a range of 4.0 and 5.6 units in the upper and lower crowns respectively, while Tree 3, the second most vigorous tree, had a range of 4.7 and 1.2, and Tree 1, the low-vigour tree, had a range of only 0.8 and 4.0 respectively.

5.4 SUMMARY

A study was made of the effect of site on the translocation of foliar nitrogen and phosphorus in needles of different ages in the upper and lower crown of three P.radiata trees of the same age but of different vigour. The sampling unit was a

fascicle of three needles.

The data suggest that the translocation of N and P may be more restricted in a tree of low than of high vigour.

The translocation of N in a low-vigour tree was more irregular and had a less consistent trend than that of P, especially in the lower crown. The same, however, did not apply to vigorous trees. Possibly, P is better translocated than N in trees of low vigour.

Seasonal fluctuation of foliar N and P per cent, especially the latter, was correlated with tree vigour.

CHAPTER 6

SEASONAL VARIATION IN FOLIAR NUTRIENTS IN A *P. RADIATA* STAND ON A FERTILISED LOW QUALITY SITE

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6.1 INTRODUCTION

In the previous chapter, it was concluded that data on foliar N and P per cent content obtained by sampling at a standard time during the year may give a misleading picture of the nutrient status of a tree. A more reliable picture of the nutrient status would be to use the seasonal patterns of foliar nutrient content which are related to tree vigour, especially those of P. These patterns take into account the range in the levels of nutrients, the times of the minima and maxima, and the degree of fluctuation (i.e., the number of highs and lows).

However, the three trees examined in the previous chapter were located on different sites, and it is unclear whether the different patterns recorded are the result of variation in tree vigour *per se*, foliar nutrient levels *per se*, or site factors other than nutrient availability.

It seemed appropriate to explore the variation in nutrient content in trees for which the nutrient supply is under some degree of control. This was done using trees in a fertiliser experiment established by H.D. Waring of the Forest Research Institute, Canberra, on a P-deficient site (Waring, 1962).

6.2 MATERIALS AND METHODS

6.2.1 The field fertiliser experiment

The investigation was carried out in a fertiliser trial located in Compartment 142 Blue Range in the A.C.T. (Appendix I). It was established by the Forest Research Institute in 1959 at an initial spacing of 3 x 3 ft (Waring, 1962). A factorial design was used for testing the factors N (4 levels), P(4 levels), K(2 levels) and S(2 levels), confounding higher order interactions with blocks of four groups of 16 plots, thus making 64 plots in all. Plot size was 33 ft x 33 ft and the central 25 trees were used for measurement. Fertiliser compounds used and levels of nitrogen and phosphorus applied were as follows:

Nitrogen (Urea)	N_1	44	lb/ac. N
	N_2	110	"
	N_3	275	"

Phosphorus (dicalcium phosphate):

P_1	27	lb/ac. P
P_2	67	"
P_3	168	"

Over the experimental area, the total N and P content of the surface soil (0-3 in) averaged 0.05 per cent and 0.0025 per cent respectively (concentrated hydrochloric acid extraction).

At the end of 1963, the growth in height and diameter of the trees in the treatment giving maximum response was three times that of the trees in the control. Dry weight production and basal area production were thirteen times and ten times respectively that of the control. The pattern of response showed a strong N x P interaction. While N alone caused a depression in growth, P alone produced a considerable increase. The addition of N and P, however, produced much better growth than either N or P alone (Fig. 6.1).

In February 1964, the area was thinned to 6 ft x 6 ft. Half the thinned area was refertilised in October 1964 at twice the original rate.

6.2.2 Methods

Four plots in a single block and containing the following treatments $N_0 P_0$, $N_0 P_3$, $N_3 P_0$ and $N_3 P_3$ were selected. It was thought that the extreme N and P regimes would provide maximum contrast in the seasonal variation of these two elements in the foliage. All plots were at the K_0 level for potassium but had been fertilised with sulphur. The latter had no effect on growth (H. Waring, pers. comm.).

Eight dominant and co-dominant trees in each plot were used, making 32 trees in all. On each tree, one vigorous branch in the third annual whorl from the tip and on the southern side of the tree was tagged with a plastic label. At each sampling, 10 to 15 fascicles were detached at random from each age section of the three-year old branch.

During the study period of Spring 1968 to Winter 1969, seven samples were taken, five from September to January because of the critical growth season (see Chapter 5). Bud break varied between plots from early spring to mid-spring. In the N_3P_0

NUTRIENT TRIAL BLUE RANGE A.C.T.

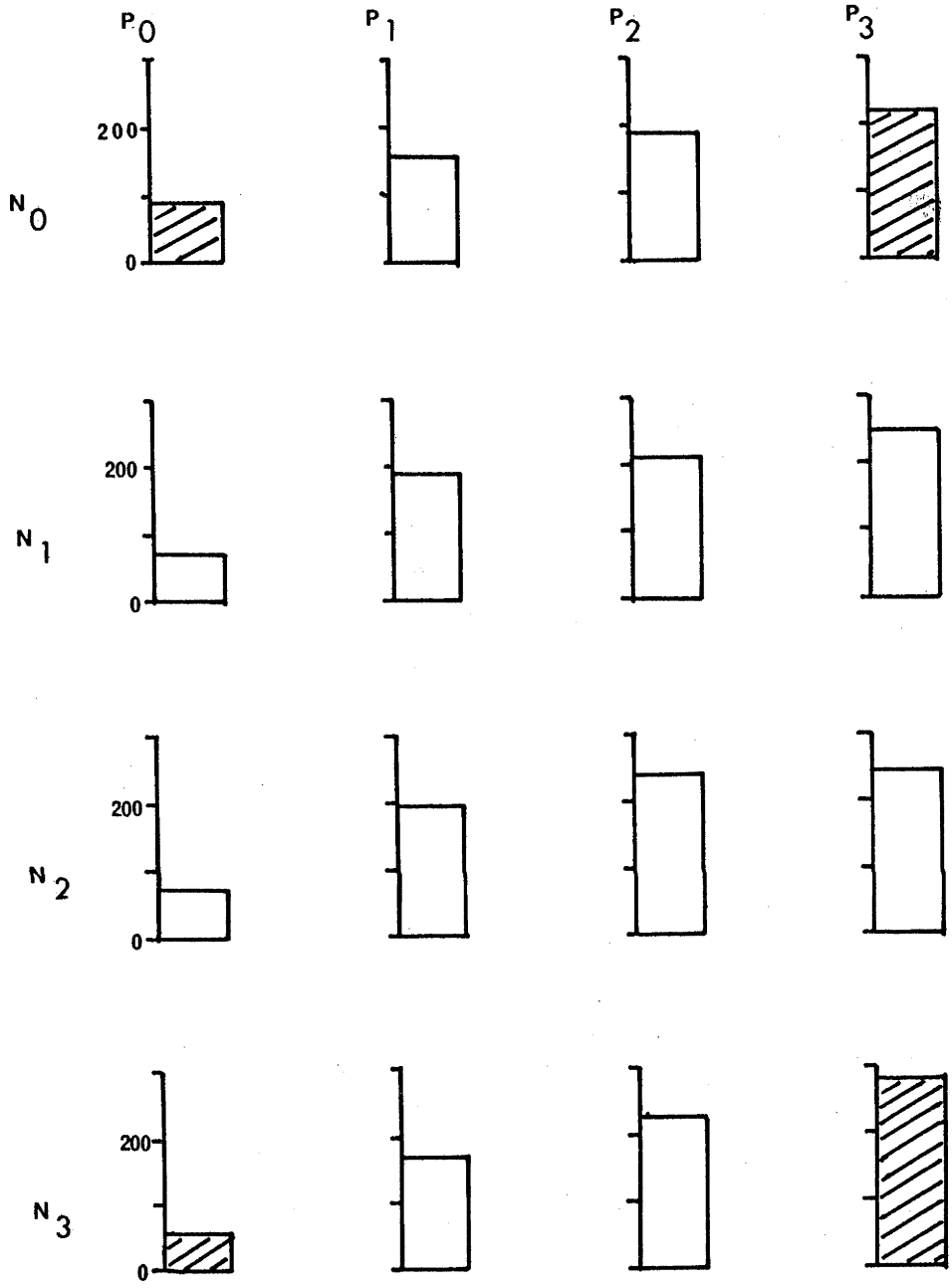

FIG 6.1 Diagram showing growth response of the nutrient trial at Blue Range, A.C.T. (Courtesy H.D. Waring of the Forest Research Institute). The vertical scale represents height (cm.) measured at age of 4 years. There are four treatment levels of N and P. The shaded columns represent the four treatment combinations selected for the present seasonal study, i.e., N_oP_o, N_oP_3, N_3P_o and N_3P_3.

treatment, the trees were so strongly suppressed by N addition in the absence of P that most of the three-year old needles were prematurely shed. Consequently, for this plot only partial data are available.

6.3 RESULTS

6.3.1 Variation in foliar phosphorus

(a) Current needles

The first samples were not taken until December because of the small size of the needles.

Over the year as a whole, the stands fall into two distinct groups, viz., N_3P_3 and N_0P_3 treatments and N_0P_0 and N_3P_0 treatments, the P supply being the controlling factor (Fig. 6.2). It is clear that in summer the P status of foliage in the four stands may be approximately the same; however, over the whole year, it clearly differs between stands.

The treatment order in terms of decreasing foliar P content is N_3P_3, N_0P_3, N_0P_0, N_3P_0 i.e., the treatments involving P fertiliser have higher foliar P levels than those without P, irrespective of N supply.

The range of fluctuation in the less vigorous stands (N_3P_0 and N_0P_0) is clearly more than that in the more vigorous stands (N_0P_3 and N_3P_3). This does not support the conclusion of the previous chapter that foliar P fluctuates more in more vigorous trees.

(b) Older needles

There is a striking uniformity in the patterns of foliar P per cent irrespective of needle age and fertiliser treatment (Figs. 6.3-6.5).

Again for any needle age, it is clear that the seasonal pattern gives a more reliable picture of the relative P status of trees than would any single sampling during the year.

There is some difference in the fluctuation of foliar P in 2-, 3-, and 4-year needles respectively. In the latter needles, the levels in all stands fluctuate widely but, for most of the year, they do not differ statistically. This suggests the need to confine sampling to 1- to 3-year old foliage.

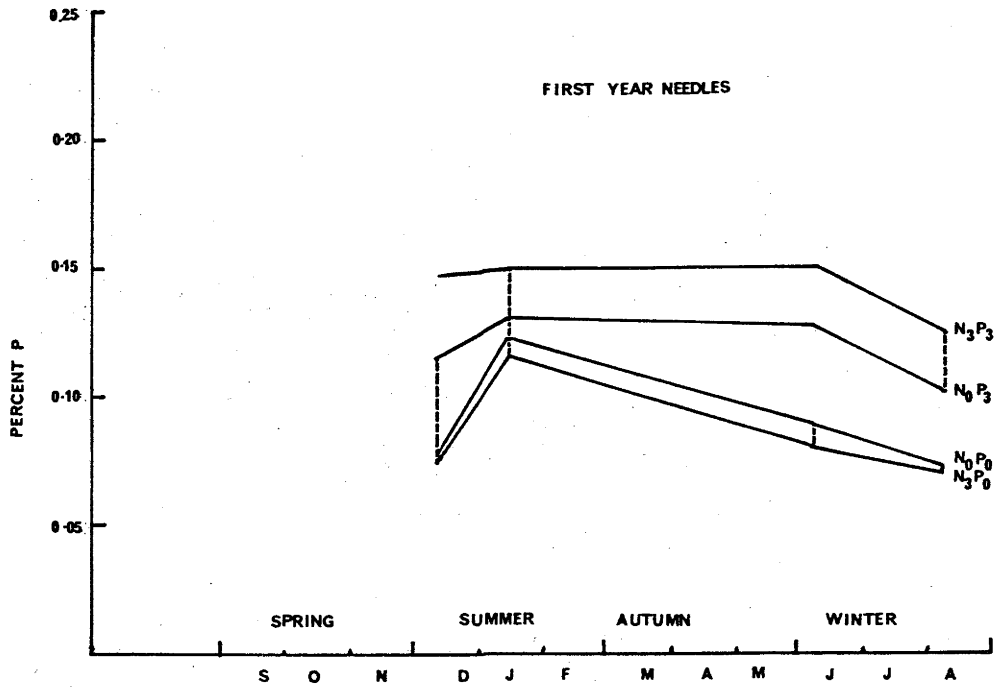

FIG 6.2

Seasonal pattern of phosphorus per cent in first year needles in stands subjected to fertiliser treatments (see Fig. 6.1). The values connected by the broken vertical line at a sampling time are not significantly different at p=0.05.

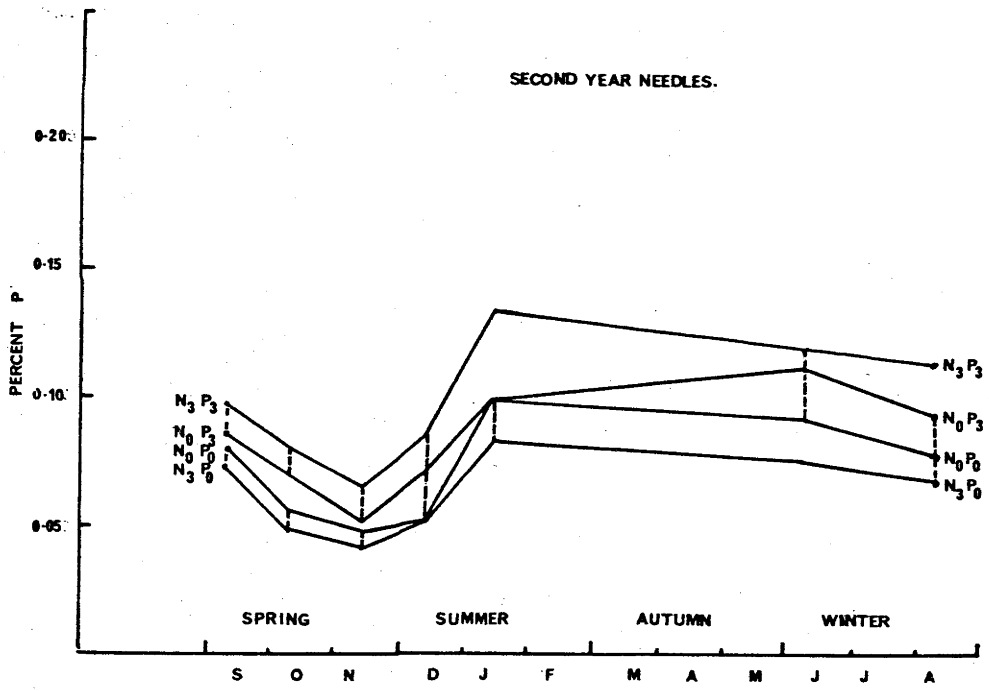

FIG 6.3

Seasonal pattern of phosphorus per cent in second year needles in stands subjected to fertiliser treatments (see Fig. 6.1). The values connected by the broken vertical line at a sampling time are not significantly different at p=0.05.

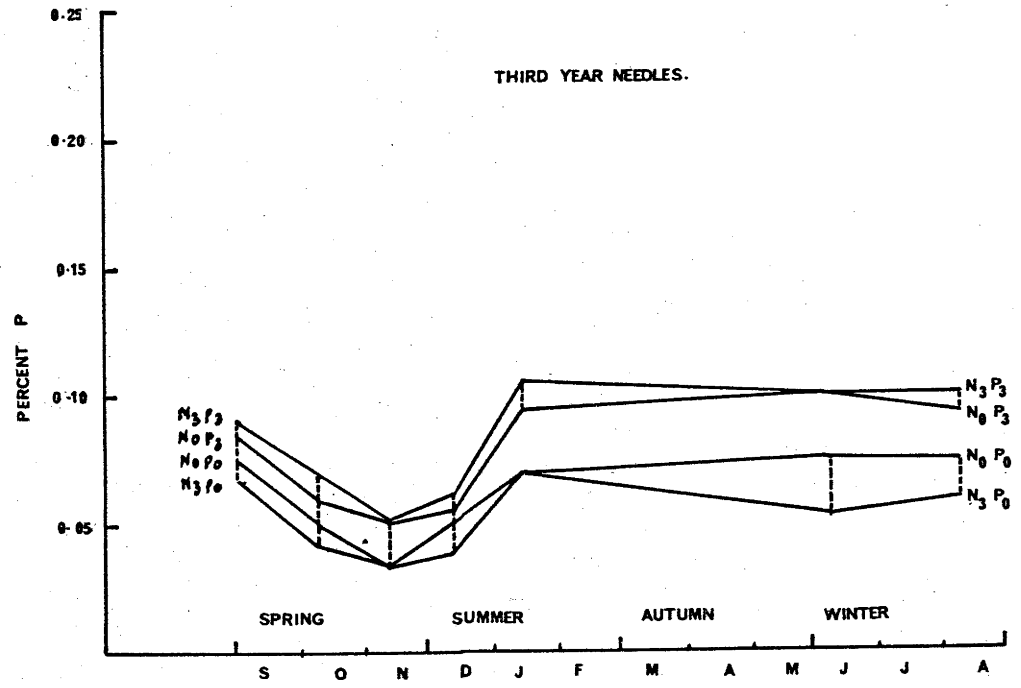

FIG 6.4

Seasonal pattern of phosphorus per cent in third year needles in stands subjected to fertiliser treatments (see Fig. 6.1). The values connected by the broken vertical line at a sampling time are not significantly different at p=0.05.

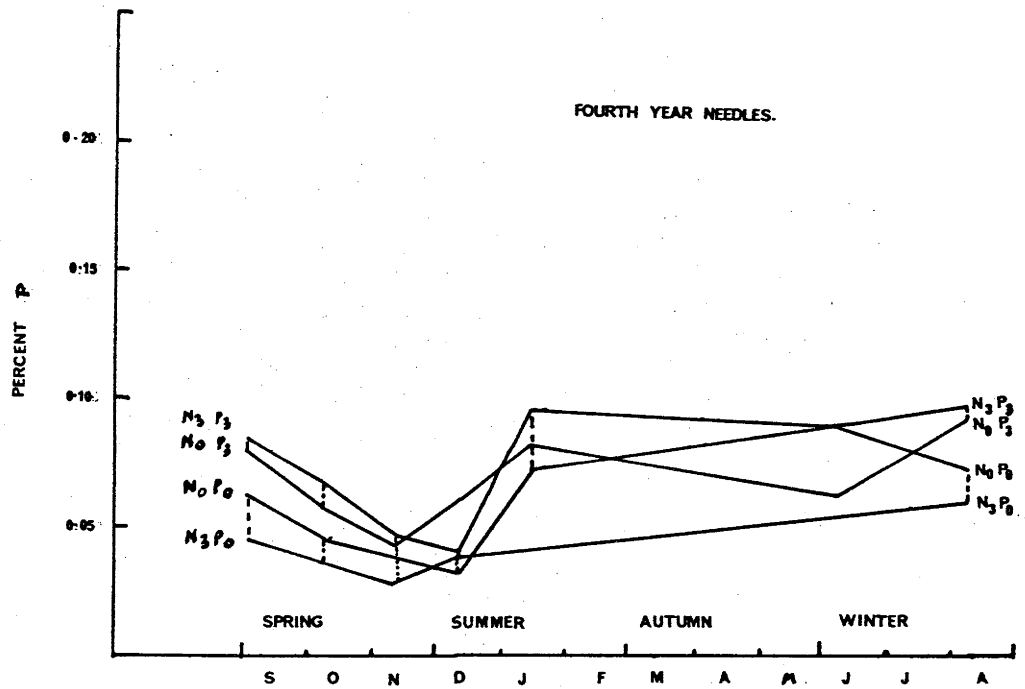

FIG. 6.5

Seasonal pattern of phosphorus per cent in fourth year needles in stands subjected to fertiliser treatments (see Fig. 6.1). The values connected by the broken vertical line at a sampling time are not significantly different at p=0.05.

In the 2- and 3-year needles, the fluctuation in the four stands is more or less the same, although it tends to be greater in the more vigorous stands. This supports the observation in the previous chapter that foliar P per cent tends to fluctuate more in vigorous stands.

The uniformity in the pattern of foliar P levels suggests that the pattern in P. radiata is either under strong genetic control or is controlled by some environmental factor other than the amount of P available for uptake and accumulation in the tree. Pattern of moisture supply could be a contributing factor as this would be common to all treatments in this study, but not to the individual trees on different soils examined in Chapter 5.

6.3.2 Variation in foliar nitrogen

The most striking features of the N patterns are:

(i) in contrast with foliar P, foliar N is highest in the less vigorous plots (those lacking phosphatic fertiliser) and tends to be higher in plots receiving nitrogenous fertiliser;

(ii) although a major growth response was obtained with added N in the presence of added P, the foliar N level in the treatment with P alone added (N_0P_3) was nevertheless above the "critical level" suggested by Raupach (1967a) for the species i.e., 1.4 per cent N;

(iii) the relatively flat foliar N / needle age gradient for needles aged 1 to 3 years is unusual, at least in terms of the data for South Australian stands (Chapter 2); and this applies to all treatments except N_3P_3 (see later).

(a) Current needles

Records of foliar N, as for foliar P, did not commence until December. N per cent rose sharply from November to December. There then appears to have been little change until the following autumn, after which foliar levels fell sharply (Fig. 6.6). At the autumn sampling, all foliar N levels were above the 1.4 per cent level. This contrasts with foliar P which was well below the critical level in those treatments which resulted in depressed growth.

As for P, the seasonal pattern as a whole and not the level at a given time of the year, clearly indicates the relative status of the trees, the increasing N status being as follows: N_3P_0, N_0P_0, N_3P_3, and N_0P_3. However, this relative N status does not reflect stand vigour; indeed, the stunted stand had the highest foliar N level most of the time.

(b) Older needles

The N patterns are markedly different from those of P and fluctuate much more widely in needles of all ages (Figs. 6.7-6.9).

For all needle ages (2-4 years), N per cent rose sharply from September through to January in those stands not receiving P fertiliser (N_3P_0 and N_0P_0). This contrasts with foliar P which fell from September to November (i.e., throughout the main growing season) before rising again. However, in the two stands receiving P fertiliser (N_3P_3 and N_0P_3), the sharp increase in foliar N during the growing season was lacking. Again, P is the controlling factor for both N level and pattern.

There is no clear indication that tree vigour affects the degree of fluctuation of foliar N although there is a tendency for it to fluctuate more in the less vigorous stands (N_0P_0 and N_3P_0 treatments). This agrees with the result of Chapter 5.

The generally similar patterns of foliar N and P per cent in all four stands irrespective of tree vigour, foliar nutrient levels per se, and N and P fertiliser supply, suggest either that foliar nutrient levels are strongly influenced by factors other than those just mentioned or they are inherent to the phenotype on this site. All the study plots were on the same soil type within a small area and would have been subject to a common regime of soil moisture, microclimate, and other edaphic factors.

6.4 DISCUSSION

The results of the present study of seasonal patterns in foliar N and P per cent in trees of varying vigour under fertiliser treatments are summarised as follows:

(1) The seasonal pattern over the whole year was a more reliable index to relative nutrient status than the

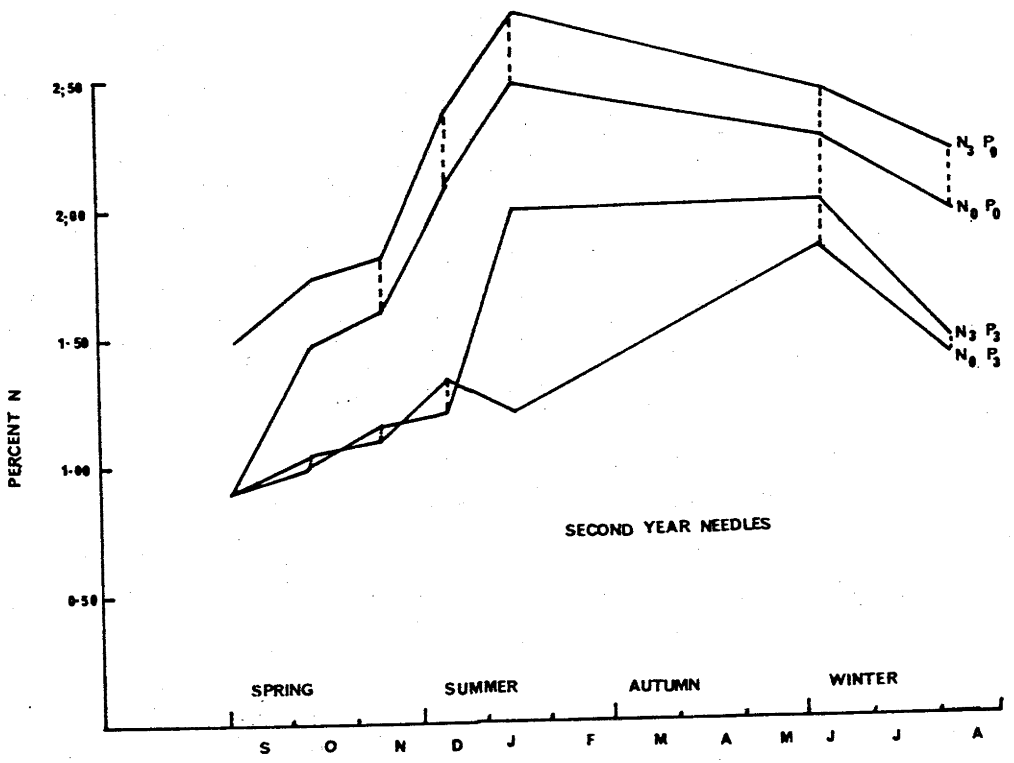

FIG. 6.7

Seasonal pattern of nitrogen per cent in second year needles in stands subjected to fertiliser treatments (see Fig. 6.1). The values connected by the broken vertical line at a sampling time are not significantly different at p=0.05.

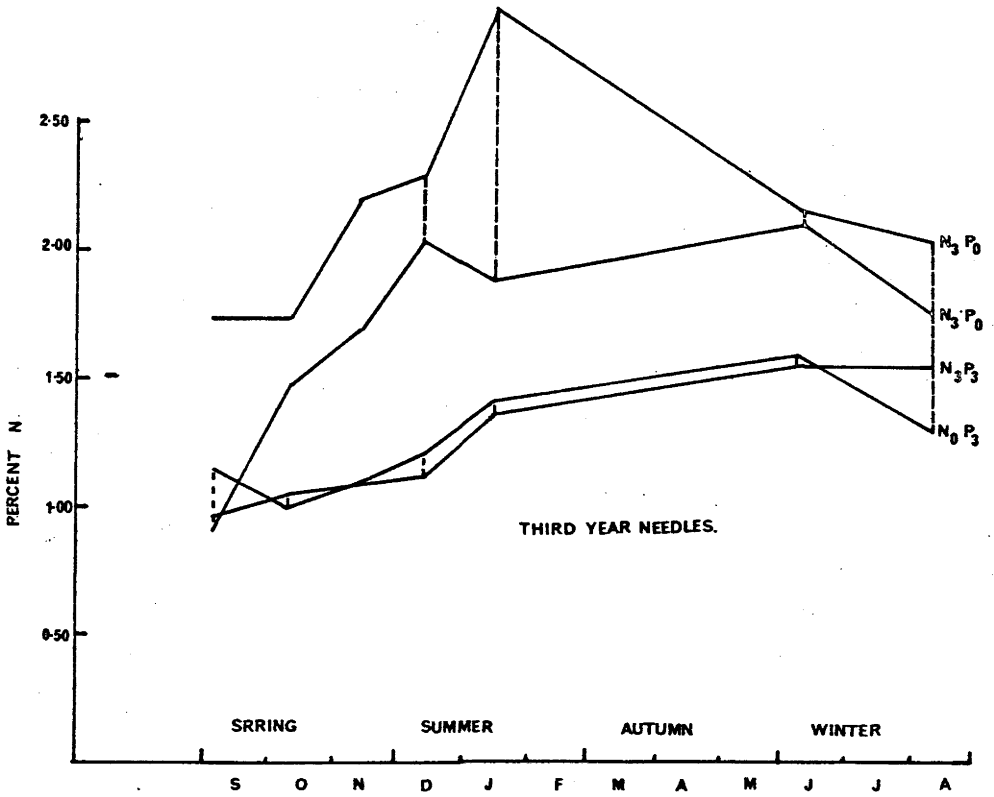

FIG 6.8

Seasonal pattern of nitrogen per cent in third year needles in stands subjected to fertiliser treatments (see Fig. 6.1). The values connected by the broken vertical line at a sampling time are not significantly different at p=0.05.

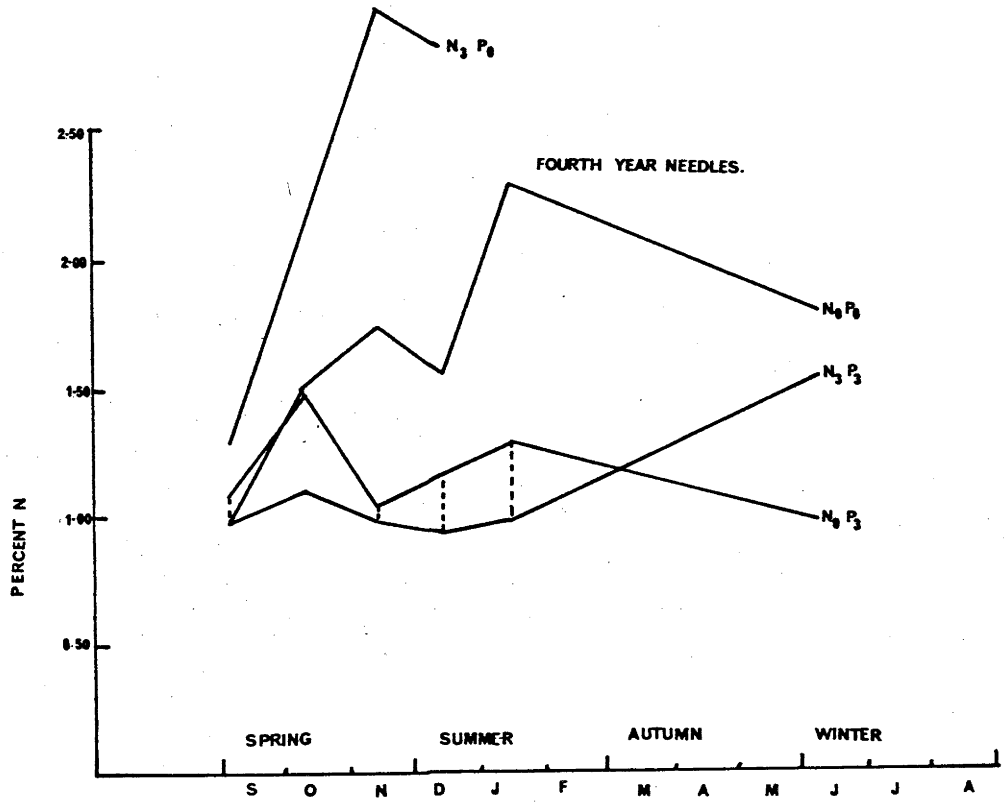

FIG 6.9

Seasonal pattern of nitrogen per cent in fourth year needles in stands subjected to fertiliser treatments (see Fig. 6.1). The values connected by the broken vertical line at a sampling time are not significantly different at p=0.05.

results of any single sampling during the year;

(2) Foliar P per cent was positively related to tree growth in contrast to foliar N which was negatively related;

(3) The extent of fluctuation in nutrient per cent was not related either to the foliar levels themselves or to N and P fertiliser supply. Fluctuation in the level of foliar P was related to tree vigour but that of foliar N was not.

Generally, these results agree with those of previous chapters that foliar P per cent is a more reliable index to tree growth than foliar N per cent.

In the previous chapter, an examination was made of the N:P ratio of foliage in different parts of the crown of P. radiata trees of varying vigour. In this study, the variation in the N:P ratio can again be used to illustrate a relationship between growth and the balance of N and P in the foliage. Table 6.1 shows the variation of the N:P ratio throughout the year in 2-year needles in the upper crown of trees in stands subjected to different fertiliser treatments:

Table 6.1

Seasonal variation of the N:P ratio in 2-year needles in the upper crown of P. radiata trees under different fertiliser treatments

Fertiliser Treatment	Spring	Summer	Autumn	Winter
N_0P_0	26.8	24.7	23.5	24.1
N_3P_0	37.2	32.7	32.9	32.4
N_0P_3	16.0	12.3	15.1	15.8
N_3P_3	14.2	12.9	15.2	14.3

The ratios throughout the year for the more productive stands (i.e., N_0P_3 and N_3P_3) are well within the suggested range of 5 - 16 for good growth of the species (Raupach, 1967a), while those for the control plot (N_0P_0) and the depressed plot (N_3P_0) are much higher than 16, viz., 24-27 and 32-37 respectively.

However, it was also mentioned in Chapter 5 that the range of variation in the N:P ratio may be a more reliable index of vigour than any single value, i.e., the larger the range, the greater the tree vigour; but this is not so in the present study where the range in the ratio for the more vigorous stands is smaller, viz.,

Stand	N:P range
N_3P_3 (vigorous)	2.3
N_0P_3 (vigorous)	3.7
N_0P_0 (non-vigorous)	3.3
N_3P_0 (stunted)	4.8

On this site, the relationship between foliar N and growth provides a striking contrast with the relationship between foliar P and growth. Phosphorus uptake is apparently a factor regulating uptake of nitrogen. The correction of P deficiency helps to regulate the N uptake so that irrespective of its supply in the soil, uptake is proportional to the amount of dry matter produced. On this particular site, once the P deficiency is overcome, foliar N is virtually unaffected by the presence or absence of added N. Where P is deficient, there is no regulation of N-uptake, so that foliar N concentration may be very high. In the absence of added P, an imbalance between foliar N and P may be as much a cause of depressed growth on the site as the low level of foliar P itself (see later).

The foliar N levels are high in all treatments, i.e., in excess of the suggested critical level for P. radiata. It is unclear why a substantial response to added N is obtained on this site once the P - deficiency is overcome. In the treatment receiving P fertiliser at the P_3 level but no nitrogen (N_0P_3), the foliar N concentration was 1.80 per cent at the June sampling of 1-year needles. This is well above the 1.40 per cent critical level and is equivalent to that of some very productive stands in South Australia (Chapter 2). Why then a substantial response to N in the N_3P_3 treatment? Perhaps a factor such as the seasonal pattern of available moisture may have a marked influence on the mobility of N in P. radiata. Where this element is not actively translocated, a particularly high level of foliar N may be

required to compensate for this immobility. Conversely, where N is actively translocated, good growth may be obtained with low foliar N concentrations; this may explain, for example, the highly productive SQII-III stands on Nangwarry Sand (Chapter 2) having a mean foliar N per cent of 1.55 and a foliar P per cent of 0.140 (winter sampling, current needles, upper crown).

When the foliar N / needle age relationship for the various fertiliser treatments is examined (Fig. 6.10), there seems to be little indication of any real nitrogen stress associated with any treatment on this site. At the winter sampling, foliar N concentration in 2-year needles was generally greater than that in the 1-year needles except in treatment N_3P_3, i.e., N per cent is greater in 2-year than in 1-year needles even where no N is added. In 3-year needles, the foliar N level varied from 1.55 to 2.15 per cent over the four treatments, compared with a range of 1.80 to 2.15 per cent in 1-year needles. There is little change in the foliar N / needle age relationship for needles aged from 1 to 3-years; this pattern differs from that of all stands examined in South Australia (Chapter 2).

The soil underlying the fertiliser experiment is shallow and has a large stone content. No studies of soil moisture have been made on this site but it is apparent that prolonged periods of limited moisture supply would be characteristic of the site. Apparently the soil moisture condition does not unduly restrict uptake of available soil nitrogen, but its mobility within the tree may be affected during the normally dry summer months.

The interaction of the seasonal moisture pattern and nutrient supply may be very important to the growth of P. radiata. An analysis of the water regime of the site may be necessary to fully appreciate the significance of foliar nutrient level. A different set of criteria for critical ranges may be needed for different soil conditions. Bengston and Voigt (1962) pointed out that the relationship between water supply and foliar nutrient concentration varied according to the availability or solubility of the nutrient in question. When the nutrient is present in the soil in an easily soluble form, foliar concentration will increase with a diminishing water supply. If the nutrient is in a less

soluble form, concentration will decrease with diminishing water supply. A few reports concerning the moisture availability/foliar nutrient interaction have been made and they can usually be interpreted in terms of a dilution effect. Hoyle (1965) examined seasonal changes in leaf content of N, K, P, Ca and Mg in yellow birch (Betula lutea Michx.) growing on well-drained and poorly-drained soils. He found that the foliar percentages of N and P were higher for trees growing on the drier soil where there was apparently greater moisture stress. Average dry leaf weights and per cent Ca and Mg were greater on the moist soil. This means that the higher levels of foliar N and P in trees growing on the dry soil may be partially due to rapid uptake of these elements when soil conditions were favourable despite the fact that dry-matter production overall was less. Schomaker (1969) showed the interaction between nutrient solution concentration and irrigation schedule was highly significant in regard to seedling weight of white pine (Pinus strobus L) and the mean N, P, K concentration showed significant increases with moisture stress. Irrigation treatment, however, had no significant effect on foliar Ca and Mg levels. Other examples include those of Walker (1962) and Hosner et al. (1965). Walker found that N, P, K levels in Loblolly pine (Pinus taeda L), Slash pine (Pinus elliottii Eng.) seedling foliage increased when the soil was maintained under normal moisture conditions as opposed to a saturated condition. Hosner et al. showed that the concentration of N and P in the tissues of certain species of broadleaf trees increased under soil moisture stress. However, the total quantity of these nutrients accumulated per seedling decreased with reduction in available water as seedling size decreased.

Clearly a research programme is needed to further investigate the growth of Pinus radiata on low quality sites, particularly the interrelationship of nutrient uptake, foliar nutrient concentration, moisture availability and growth response to various combinations of fertilizers. For example, it would be interesting to know whether response to the N_0P_3 treatment with superimposed irrigation would be equivalent to the N_0P_3 treatment with added N fertiliser (i.e., the N_3P_3 treatment); and it would

be interesting to know how irrigation on this site influences the mobility of nutrient elements, particularly nitrogen, in both the upper and lower crown. The variation in foliar nutrient status and nutrient mobility in trees as described in Chapter 5 might be interpreted in terms of both soil nutrient and moisture availability. For example, on the site carrying the vigorous Tree No.3, both water and soil nitrogen may be in ample supply but not phosphorus; phosphorus availability may have been inadequate to regulate N-uptake, so that large amounts of foliar N were accumulated in the tree.

6.5 SUMMARY

A study was made of seasonal variation of foliar N and P in P. radiata trees of varying vigour, under fertiliser treatment on a uniform P-deficient site in the A.C.T.

The results are as follows:

(1) The seasonal pattern over the whole year was a more reliable index to relative status of nutrient than the results of any single sampling during the year;

(2) Foliar P per cent was positively related to tree growth in contrast to foliar N which was negatively related;

(3) The extent of fluctuation in nutrient per cent was not related either to the foliar levels themselves or to the N and P fertiliser supply. Fluctuation in the level of foliar P was related to tree vigour but that of foliar N was not.

The contrasting relationship of foliar N and P to tree growth, and the apparent controlling effect of P supply on foliar N are discussed. It is suggested that, on this low quality site, moisture supply and foliar nutrient level interact in affecting tree growth.

CHAPTER 7

GENERAL DISCUSSION

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7.1 FOLIAR N AND P LEVELS AND TREE GROWTH

In studies on foliar N and P in stands showing a marked response to N and P fertilisers, Waring (1964) concluded that foliar P may be a more reliable index of treatment response than foliar N. This is supported by data obtained from unfertilised stands in the south east of South Australia (Chapter 2). Apart from a lower value in Site Quality V stands, foliar N levels tend to be more uniform than those of foliar P over the site quality and stand age range examined. Distinctive N horizontal gradients are not apparent in any site quality class and the gradients associated with different environments, with few exceptions, are more or less parallel. Foliar N is therefore less sensitive to variations in production and stand age than foliar P.

That there is a NxP interaction in the response of P. radiata to fertiliser treatment is well proven (Waring, 1962, 1969). However, the way in which the foliar N and P levels are controlled by this interaction, is not clear. According to Waring (1968), the foliar P level generally rises when P fertiliser is applied, and the presence of added N affects this response in two ways: (a) at low levels of applied or available P, the percentage content of P in the foliage declines at higher levels of applied N; and (b) at high levels of applied or available P, the percentage content of P increases with increase in applied N.

The foliar N content generally increases at higher rates of application of nitrogenous fertiliser and decreases when an increased application of P leads to a positive growth response.

However, there may be a strong controlling effect of P supply on the foliar N level of trees growing on a P-deficient site, as demonstrated in Chapter 6. On this particular site, once the P deficiency was overcome, foliar N and the N:P ratio were only slightly affected by the presence or absence of added N. Thus, where P is deficient or not available in adequate amount, it would seem that there is no regulation of N uptake and the foliar N content may be high.

In assessing how well foliar N and P are related to growth, it should be borne in mind that many environmental factors simultaneously affect growth. Therefore a simple relationship between foliar N and P and growth is unlikely. A good example of the interrelationship between the physical and chemical factors of the environment and growth is provided by the work of Czarnowski, Humphreys and Gentle (1967) for P. radiata in N.S.W.. Using soil and climatic data from a group of plantations, they derived an equation expressing site index as a function of soil and climatic variables (from an amalgamation of the Mitscherlich equation and the Czarnowski frame equation - Czarnowski, 1964). It was most evident that the omission of any one variable brought about an over-simplification of the relationship to the point where total error became excessive.

In view of the many factors involved, it is not surprising that Raupach, Boardman and Clarke (1969) could apportion only approximately 50 per cent of the variance to foliar N and P in relating foliar nutrient levels to the height growth of P. radiata in South Australia.

In studies of coniferous foliar nutrient levels, it is customary to determine the critical or threshold levels associated with acceptable or good growth. However, it is probable that a single general critical level may be misleading, because under different environmental conditions different sets of critical levels might apply, e.g., on a dry site, the critical levels of foliar N and P may be higher (cf. Walker, 1962; Hosner et al., 1965; Schomaker, 1969). In Chapter 6, P. radiata on a presumably dry, low-quality site showed additional response to nitrogenous fertiliser even though foliar N levels in the stand were higher than the critical level of Raupach (1967a). Perhaps a good supply of moisture and moisture movement is needed to translocate nitrogen and make it more active within the plant (see later).

This interaction of water supply and foliar nutrient level is apparently important in determining water economy and maximum photosynthetic rate. Keller (1967, 1968) showed for

Populus nigra that the foliar nutrient levels associated with maximum photosynthesis and the most economic water use respectively do not coincide. Thus, the desirable nutrient content of foliage may vary somewhat according to the moisture regime of the site. Keller found that the optimum photosynthetic rate occurred in leaves with 3 per cent N, but optimum water economy in leaves with 3.6 per cent N.

Clearly, as suggested earlier, a research programme is needed to examine further the growth of P. radiata on low-quality sites, particularly the interrelationship of foliar nutrients, water supply and growth using various combinations of fertilisers. It would be interesting to know much more of the interaction of irrigation and fertiliser treatment on growth. For example, on Waring's plots, would adequate irrigation provide a response similar to that of added nitrogen once the primary P deficiency is overcome?

In studying foliar nutrient levels in stands of different age, it is important to know the influence of stand age per se on foliar N and P. In other words, are there different optimum levels at different ages? Comparing the optimum levels of seedlings and adult trees, it would seem that the optimum level decreases with age. However, whether this decrease is due to physiological ageing is not clear (Tamm, 1964). Results presented in Chapters 2 and 4, and the work of Forrest (1969), Höhne (1963), Höhne and Nebe (1963) and Fielder, Wunderlich and Höhne (1967), illustrate that foliar nutrient levels are a function of both stand growth rate and nutrient supply, especially at the time of peak demand i.e., at crown closure. Although the nutrient levels of comparable foliage may vary greatly from year to year when the nutrient supply is adequate (Humphreys and Kelly, 1962; Miller, 1966), there is little evidence of a lowering of the levels with tree age over a long period. For example, the foliar N and P levels for pines in Germany remained more or less constant from 10 to 100 years (Fielder, Wunderlich and Höhne, loc. cit.). In fact, Romel (1957) suggests that the well-known decrease in forest yield at advanced ages may be caused more by nutrient

deficiency than by physiological ageing or respiratory losses. In South Australia a SQ V stand on Mt Burr Sand showed a falling nutrient level in needles as they aged in contrast to a stable level in a SQ II stand on Wandilo Sand (Chapter 2). In an age series on a poor site in the A.C.T. (Chapter 4), variation in foliar N with age was not significant, but the level of foliar P was highest in a very young stand, lowest at the time of peak nutrient demand (crown own closure) and intermediate in older stands. In brief, foliar nutrient levels are a function of growth rate and nutrient supply.

At any age well past the time of peak nutrient demand, foliar N and P levels in current needles of P. radiata may be more or less constant for a given site (Chapter 2). Hence, in such stands, nutrient levels in current needles may be useful in assessing the current nutrient status of trees. These levels, however, are not necessarily an infallible guide to the tree's nutritional status. The results of the research reported here suggest that a reliable assessment of tree nutrient status depends as well on an understanding of the variation in and significance of both the vertical and horizontal gradients in foliar nutrient levels.

7.2 PATTERNS OF FOLIAR N AND P IN THE CROWN

The gradients of foliar N and P observed in the crown of P. radiata (Chapters 2, 3 and 4) can be summarised as follows:

(a) In the plantations of south-east South Australia, the horizontal nutrient gradients in the upper crown, especially of P, are characteristic of different soil types. What does this gradient from current to older needles mean? Firstly, the presence of such a gradient could mean a better translocation of nutrients to actively growing tissues (see later). Secondly, the horizontal gradient might be used to detect potential nutrient stress e.g., the steeper the gradient, the greater the possibility of a developing nutrient stress, especially when deviations from an observed normal gradient are noted.

(b) In four stands of varying vigour on two contrasted soils in the A.C.T. (Chapter 3), no difference between stands in the horizontal gradients of N and P was observed, and although a vertical gradient for N and P was not detected in two low-vigour stands, one was found in two vigorous plots.

(c) Within an age series on a low-quality site in the A.C.T., the only vertical gradient recorded was for P in the youngest stand. No significant vertical gradient for N was detected in any stand. In this age series, the youngest stand was the only one which could be regarded as still developing vigorously at 7½ years of age.

These three studies suggest that the presence of strong vertical gradients in foliar nutrients might be related to stand vigour. An examination of the literature on such gradients in tree crowns is summarised in Tables 5.1 and 5.2. This does not indicate any inherent patterns in the concentration of foliar N and P in tree crowns, and suggests that site may influence the internal distribution of N and P in the crown, possibly through differences in translocation.

This hypothesis was tested in Chapter 5 where it was shown that:

(a) Translocation of N and P is less efficient in trees of low vigour; and also

(b) In trees of low vigour, N may be more poorly translocated than P.

Having established that translocation of N and P are in fact related to tree vigour (and possibly other factors of the environment), the patterns of seasonal variation in foliar N and P levels were considered. It was concluded that the vertical gradient pattern of these nutrients was not necessarily a good index of tree vigour or of the translocation of nutrients; rather, the extent and range of fluctuation in the nutrient level at specific locations seemed a better guide to tree vigour and translocation. The extent of seasonal fluctuation can be considerable and throws doubt on the meaningfulness of any single sample during the year as an index of tree nutrient status,

particularly with respect to some "critical level". This was established convincingly in Chapter 6. The seasonal pattern is a much better index to nutrient status.

The extent of seasonal fluctuation in N and P was further studied in Chapter 6. It was shown that the extent of fluctuation was independent of either foliar nutrient levels *per se* or N and P fertiliser supply; but while the fluctuation in foliar P was positively correlated with tree vigour, that of foliar N was negatively correlated. Here again, foliar P seems to be more reliable than foliar N as an index of tree growth.

The above results and observations prompt the hypothesis that where moisture is limiting, N movement in the tree may be restricted, critical foliar levels may be higher (than when translocation is efficient), and the lack of foliar N gradients in stands on low-quality sites may reflect a limited translocation of N influenced by the limiting moisture supply. While further research is needed to confirm the hypothesis, it is likely that a tree in which the nutrient levels are adequate and the nutrients are being used efficiently, might have:

(1) a moderate rather than a steep horizontal nutrient gradient;
(2) a vertical nutrient gradient; and
(3) a strong seasonal fluctuation in foliar nutrient levels.

7.3 SIGNIFICANCE OF THE FOLIAR N:P RATIO

The N:P ratio of needles has been advocated as an index of good growth for many species. For example, Van Goor (1953) suggested values from 9.2 to 11.5 for *Larix leptolepis*, Bószörményi (1958) 5 to 15 for *Pinus sylvestris*, Richards (1961) a minimum of 10.4 for *Pinus taeda*, and Raupach (1967a) a range of 5 to 16 (optimum about 10) for *Pinus radiata*. However, as discussed earlier, use of the ratio as a growth index might be misleading due to possible changes of the N and P levels with needle age, crown position and environmental conditions, and differential translocation in the crown on low-quality sites.

Also, the use of seasonal fluctuation in the range of the ratio as an index of tree vigour was inconclusive (Chapters 5 and 6).

Nevertheless, there is no doubt that the foliar N:P ratio plays a distinct role in the metabolism of plants. For example, Keller (1968) demonstrated maximum photosynthesis and transpiration in Populus nigra leaves which were neither deficient in N (>1.9 per cent) nor P (>0.3 per cent), the N:P ratios being between 5 and 10.

Clearly, measurements of gaseous exchange may make a valuable contribution to research on forest nutrition if it is possible to determine the levels of foliar nutrients necessary for maximum photosynthesis and optimum water economy.

7.4 EFFECTS OF SITE ON DRY MATTER PRODUCTION

In this study of environment/growth/foliar nutrient interrelationships, data on the relationship between site and growth also contribute to an understanding of the way P. radiata stands develop.

The association of the particular development of a tree crown and trunk with soil type (e.g., coarse branching on certain fertile heavy soils) may be related to the influence of the environment (nutrient supply, water regime, etc....) on the growth and development of P. radiata. Fielding (1960) has described the differences in development of stands growing on contrasting soil types in the south-east of South Australia: stands of approximately the same height growth differed markedly in branching and cone production.

However, most studies of tree quality in P. radiata have been concerned with stem form parameters. Branching and cone production have been considered in so far as they affect stem quality but not in terms of the distribution of the biomass amongst tree components in individual trees or per unit area (Jacobs, 1938, 1954; Fielding, 1953, 1960, 1967b; Fielding and Brown, 1961; Beekhuis and Will, 1965; Wright, 1968; Wright, Marks and Minko, 1967).

It has been shown that marked differences occur in branch size and number (for individual trees or per unit area) between comparable stands on contrasting soils in the A.C.T. (Chapter 3). This effect of soil type on branch production is consistent with the findings of Bannister (1962) in New Zealand but somewhat at variance with those of Fielding (1960) for a similar study in the A.C.T. The negligible differences reported by Fielding are probably due to the environmental range studied being insufficiently great. Evidence is also presented suggesting that trees of similar basal area have a similar weight of foliage and of branch and bole wood irrespective of variation in soil type, site quality and tree crown characteristics (Chapter 3). The exception was a low-quality stand approaching a spindle condition.

The relationship between the bole weight and foliage weight of a stand varies with age. However, at a given age (up to about 12 years), the ratio of bole weight to foliage weight for such different stands as occur at Tumut, N.S.W. (Forrest, 1969) and Kowen, A.C.T. (Chapter 4) is similar (Fig. 7.1), despite a large variation in site quality and environmental conditions. Therefore, production of a given weight unit of bole wood on poor sites does not require any more foliage than on a good site. This may be one reason why P. radiata is capable of producing acceptable yields on a wide range of sites in Australia (Scott, 1960). It also suggests a strong genetic control on the pattern of growth in P. radiata in terms of the distribution of biomass amongst the various tree components.

However, the ratio of bole weight to foliage weight of a high quality stand of the species in New Zealand, calculated from data extrapolated from Ritchie (1968), is appreciably lower at a given age than that of both Tumut and Kowen stands (Fig. 7.1). Is this a regional environmental difference? Clearly, this cannot be answered without further research. It is interesting to note that Pinus taeda L. on a good site in southern U.S.A. has a bole weight to foliage weight ratio considerably greater than that of P. radiata at both Tumut and Kowen up to the age of about 12 years, but after 20 years, the ratio is similar to that quoted for P. radiata in New Zealand (Switzer, Nelson and Smith, 1966, 1968).

So far the effects of soil type and climatic regime have been mentioned in conjunction with variation in site quality (SQ), but what is the effect of SQ per se? The remainder of this discussion examines the effect of SQ on foliage and branch production and accumulation in the light of the data summarised in Table 7.1.

Foliage production and accumulation

Forrest (1969) surveyed the then available data and favoured the view of "relatively uniform weight of foliage production in Radiata pine stands after canopy closure over a wide range of site conditions." However, Fig. 7.2 shows that after canopy closure, the relationship between foliage weight per unit area and SQ is parabolic, increasing with increase in SQ. The data plotted in Fig. 7.2 with one exception, refer to stands with a stocking density of 1200-2000 stems per hectare The exception is the stand of Will (1964) of about 3000 stems per hectare.

Fig. 7.2 also illustrates a sharp drop in the weight of foliage in stands at about the time of canopy closure, and the lower the SQ, the greater the proportional drop. The weights of foliage in three stands before canopy closure (about 12 years of age) are plotted as triangular dots. This decline of foliage weight with time is further illustrated in Fig. 7.3. Only the high site quality stand in New Zealand does not show any sign of a declining foliage weight with age. A comparison of the way the foliage weight patterns vary with stand age again suggests a broader regional effect, i.e., the patterns for Kowen and Tumut in Australia are similar whereas the pattern for New Zealand is vastly different.

Obviously, more data covering a wider time span and range of site quality and climatic conditions are needed to reach a definite conclusion as to the effect of site on the way a stand grows. Nevertheless, in summary, the following conclusions are

Table 7.1

Production[x] of foliage and branches by P. radiata on a range of sites ('000 kg. per ha.)

S.Q.[xx]	Age (years)	Stems/ha.	Foliage	Branch	References
I	18	1700	c 13	c 26	Will (1966)
II+	3	c 2000	7.6		Ritchie (1968)
	8		c 7	c 12	
	14		c 16	c 30	
	18		c 16	c 50	
	26		c 16	c 40	
II	12	c 3000	10	10	Will (1964)
II	14	1400	8	23.9	xxx (Shannon's Flats)
III	3	1600	0.4	0.2	Forrest (1969)
	5	1500	1.9	1.2	
	7	1450	11.2	14.9	
	9	1500	8.4	9.9	
	12	1500	9.2	18.7	
IV	14	1700	7.6	29.5	xxx (Shannon's Flats
	16	1800	6.5	19.6	xxx (Pierce's Ck.)
V	8	1200	10	16.8	Forrest (1969)
V-	16	1600	4.7	12.1	xxx (Pierce's Ck.)
VI-	7½	1200	8.8	11.6	xxx (Kowen)
	11½	1500	5.7	6.9	
	14½	1200	6.3	9.9	
	17½	1500	4.1	7.7	

x Values given by author(s) or estimated, using annual increment rate (marked by c)

xx Site quality given by author or estimated according to Jacobs (1962)

xxx The present study sites in the A.C.T.

reached:

(1) in stands which have closed canopy, foliage weight increases with increase in site quality;

(2) a greater decline in foliage weight with age occurs on poorer sites; and

(3) stocking density possibly strongly influences foliage weight, especially on low-quality sites such as examined in Chapter 4.

All these factors provide some evidence that foliage weight per unit area of P. radiata is not independent of stand age, site quality or stocking density over a wide range of these three parameters. This is in direct contrast to the findings of Satoo (1967) for Pinus densiflora. Satoo showed foliage weight per unit area to be relatively independent of both stand age and site quality over a considerable range of both.

Branch production and site quality

Satoo (1967) demonstrated for Pinus densiflora that the total weight of branch wood per unit area increases slowly with age, but is dependent on stand density, particularly at stockings below 4000 stems per ha. Fig. 7.4 shows that the branchwood weight per unit area of P. radiata stands after canopy closure (12 years of age) is a function of site quality (see also Table 7.1). The resulting curve is one with a "diminishing return". Plotted values generally fit the curve well. Environmental conditions and soil types may be responsible for the high branchwood production at Shannon's Flats (Chapter 3) and in New Zealand (Ritchie, 1968), while stocking density may be responsible for the low value of Will (1964). All stands represented in Fig. 7.4 have a stocking density of 1200-2000 stems per ha., except for that of Will which has 3000 stems per ha.

Thus, branchwood production of P. radiata stands after canopy closure tends to increase with increasing site quality although soil type and, possibly, climatic conditions may alter the trend. Again, more data covering a wider range of sites, stocking densities, and climatic conditions are necessary to form a more comprehensive picture.

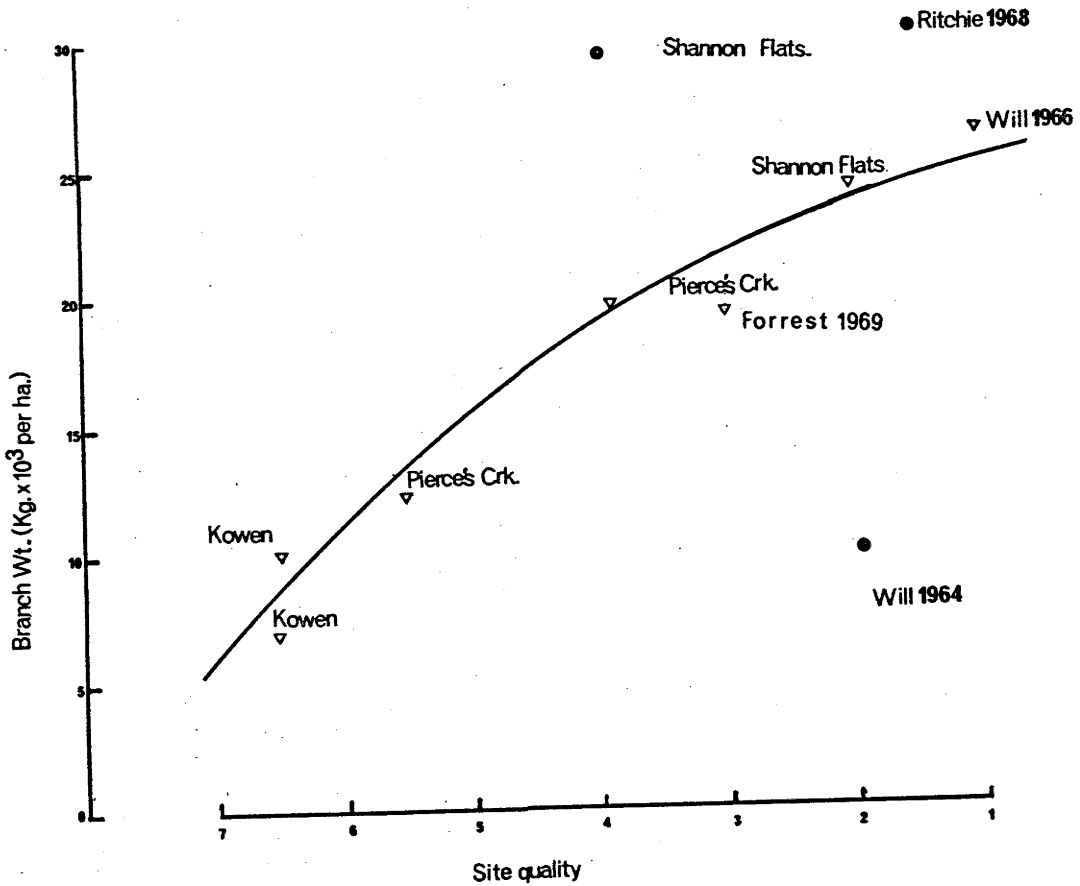


FIG 7.4

Relationship between branch weight and site quality in P. radiata after canopy closure (ca. 10 years of age). Note the three odd values represented as circular dots. (See also Table 7.1).

APPENDIX I

1. Meteorological data for study sites in the A.C.T. and southeast South Australia.
2. Dry weight estimation
3. Analytical methods for estimating total nitrogen and phosphorus in pine needles

1. Meteorological data

1.1 A.C.T. sites

The Australian Capital Territory (A.C.T.) is located in New South Wales about 200 miles south of Sydney and 100 miles inland. Its total area is 911 square miles. Canberra has a latitude of 35° South and a longitude of 149° East. Conversion of the non-commercial eucalypt forest types is the basis of softwood (mainly Pinus radiata) plantations. The objective is for 40,000 acres of softwood plantations. By 1969, 28,000 acres of plantation were under P. radiata.

The four study sites in the A.C.T., namely, Pierce's Creek, Shannon's Flats, Blue Range, and Kowen are indicated on the relief map of the territory (Fig. A.1). The altitudes are approximately 2,600, 3,000, 3,500, and 2,500 feet above sea level respectively. Climatological data for Canberra and Bulls Head (see map), and for the study sites where possible, are presented to give an idea of climatic conditions.

Briefly, the whole area is within the uniform rainfall zone. Average annual rainfall for Canberra is 25 in. Apart from topography (Fig. A.1) and a rather low level of natural soil fertility, the major factors affecting land use are climatic ones. These are low rainfall and uncertain distribution during the warmer months, and the relative short growing season owing to frost occurrence in late spring and early autumn. The climatic data for some A.C.T. study sites are summarised in Tables A.1, A.2 and A.3 (see also White, 1954).

1.2 Southeast South Australia

Climatic data for Mt Gambier, the regional capital, are presented below and in Table A.4. All sample plots in the study were located within 40 miles of Mt Gambier.

	Mt Gambier
Longitude	141° East
Latitude	38° South
Altitude	138 ft.
Average annual rainfall	31 in.
Average annual evaporation (Australian pan)	49 in.
Average daily maximum temperature of hottest month	76° F
Average daily minimum temperature of coldest month	42° F
Highest temperature recorded	104° F
Lowest temperature recorded	25° F

Table A.1

Climatic Data for the A.C.T. Study Sites.

	Canberra	Bulls Head
Longitude	149° E	149° E
Latitude	35° S	35° S
Altitude (ft)	1906	4320
Average annual rainfall (in.)	25	45
Average annual evaporation (in.) (Australian pan)	48	40
Rainfall distribution	uniform	uniform
Average daily max. temperature of hottest month	82° F	67°F
Average daily minimum temperature of coldest month	34° F	28° F
Highest temperature recorded	107° F	95° F
Lowest temperature recorded	18° F	10° F

Table A.2

Average monthly and annual rainfall for some stations in A.C.T. (points)

Location	Record Period	J	F	M	A	M	J	J	A	S	O	N	D	Year
Kowen forest	1931-60	244	210	219	202	206	214	180	202	182	280	236	239	2614
Pierce's Creek	1931-60	266	222	283	243	246	269	248	276	229	330	268	221	3101
Condor farm	1910-52	241	312	321	306	296	268	368	329	293	380	391	185	3690
Bull's Head	1940-54	368	236	336	362	446	372	270	267	387	466	376	241	4127

Table A.3

Average monthly mean, maximum and minimum temperature (^{o}F) in the A.C.T.

Location	Temperature parameter	J	F	M	A	M	J	J	A	S	O	N	D	Year
Canberra	Mean	69.1	68.4	64.3	56.3	49.6	44.3	42.8	45.3	50.1	55.7	61.7	66.2	56.1
(1928-65)	Max.	88.2	80.7	76.2	67.0	59.3	33.2	51.8	55.1	61.2	67.0	73.1	79.0	67.0
	Min.	56.1	56.0	52.5	45.5	38.9	35.5	33.8	35.5	39.0	44.3	48.9	53.4	44.9
Bull's	Mean	58.8	58.2	56.9	48.4	42.4	37.6	36.1	36.9	42.8	46.4	51.5	58.0	47.8
Head	Max.	69.2	68.0	66.1	56.5	48.8	43.6	42.2	44.0	50.6	54.9	60.9	68.6	56.1
(1945-54)	Min.	48.3	48.3	47.7	40.3	35.8	31.7	30.0	29.8	35.0	37.8	42.0	47.5	39.5

Table A.4

Monthly distribution of rainfall and temperature for the period 1911-1940 at Mt Gambier

A : Average daily maximum temperature (^{o}F)
B : " " minimum " (^{o}F)
C : " " monthly rainfall (points)

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
A	74.2	75.0	72.7	66.5	61.4	57.0	56.2	58.1	61.1	65.0	68.3	71.9	65.7
B	55.5	54.8	52.4	49.5	46.4	43.5	42.4	43.1	45.1	49.9	49.6	52.0	48.3
C	93	122	117	214	290	355	349	344	291	210	156	145	2886

Reference : Forestry Handbook, Woods and Forests Dept., South Australia. Bull. No.6.

Rain falls mainly in winter and the annual or even the monthly rainfall figures are, by themselves, a poor index of the agricultural potential of South Australia. The summer drought produces a water deficit in many South Australian soils (Chapter 2).

2. Dry weight estimation

Whenever possible, foliage samples were dried within 24 hours of collection at 70°C for 48 hours, and branch, cone and stem materials at 85°C for extended periods until a constant weight was reached. Delays in drying were sometimes inevitable, e.g., when collection sites were distant from the laboratory or the oven-drying facilities were inadequate. For P. radiata samples, Forrest (1968) reported that branchlets lost up to 8% of initial dry weight when stored for extended periods either at room temperature or in a cold room at 7°C, presumably as a result of continued respiration. He found that branchlets could be stored in the open for 7 days or at 7°C for 17 days before losses exceeded 2% of initial dry weight, and that the dry weight of branchlets oven-dried at 105°C was 2% lower than of branchlets dried at 70°C. 70°C was used in this study to avoid possible volatilisation of nitrogen, especially from foliar samples.

3. Analytical methods for estimating total nitrogen and phosphorus in pine needles

All samples were dried, finely ground in a laboratory mill, and analysed for total nitrogen and phosphorus using a Technicon Auto-Analyser and the methods adapted for it (Williams and Twine, 1967). These techniques have been widely used (e.g., Snowdon, 1967).

Briefly, for nitrogen, the sample is digested by a modified Kjeldahl procedure. Ammonium in the digest is determined by an automatic procedure adapted from Logsdon as mentioned in Williams and Twine (loc. cit). The method utilizes the blue colour formed by the reaction of ammonia with hypochlorite and phenol as a basis for the colorimetric determination of ammonia. Phosphorus is determined from the same Kjeldahl digest using a procedure adapted from Colwell (Williams and Twine, loc. cit).

The method depends upon the formation of phosphomolybdate and its reduction to molybdenum blue by abscorbic acid.

Figure A.I (Appendix I)

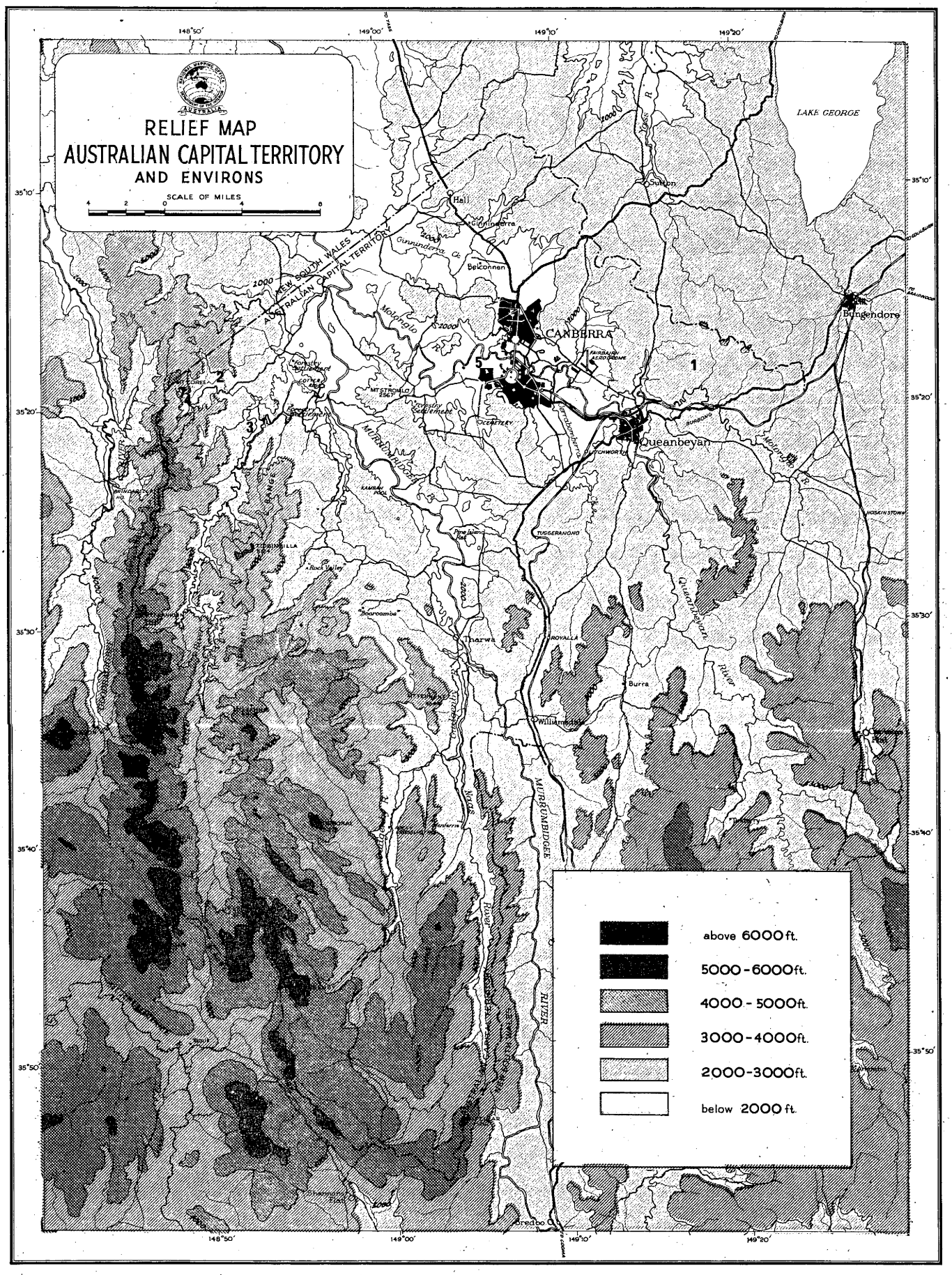
The location legend of sites marked on the accompanying map is as follows:

Study sites

1	Kowen forest
2	Blue Range
3	Pierce's Creek (near Vanity crossing)
4	Shannon's Flats

Meteorological stations

5	Canberra
6	Bull's Head
7	Condor farm


RELIEF MAP
AUSTRALIAN CAPITAL TERRITORY
AND ENVIRONS
SCALE OF MILES
4 2 0 4 6
148°50'
149°00'
149°10'
149°20'
35°10'
35°20'
35°30'
35°40'
35°50'
LAKE GEORGE
Sutton
Hall
Gininderra
Ginninderra Ck.
Belconnen
Molonglo R.
CANBERRA
FAIRBAIRN AERODROME
Bungendore
Queanbeyan
Jerrabomberra
Yarrowlumla
Tuggeranong
Tharwa
Royalla
Burra
Williamsdale
Murrumbidgee River
Queanbeyan River
Mt Stromlo 2567
Forestry Settlement
Cotter R.
Cotter Dam
Gudgenby R.
Naas R.
Orroral R.
Tidbinbilla
Rendezvous Creek
Boboyan
Bredbo
Shannons Flat
NEW SOUTH WALES
AUSTRALIAN CAPITAL TERRITORY
above 6000 ft.
5000 - 6000 ft.
4000 - 5000 ft.
3000 - 4000 ft.
2000 - 3000 ft.
below 2000 ft.

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